

# POLLEN MORPHOLOGY: THE POTENTIAL INFLUENCE IN HIGHER ORDER SYSTEMATICS<sup>1</sup>

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## ABSTRACT

The pollen of approximately 650 species from at least 25 families has been examined in LM and SEM, and a representative number in TEM. These families include those found in the orders: Centrospermae, Plumbaginales, Polygonales, Primulales, Ranunculales, and Dilleniales. Evidence from pollen morphology: reinforces the close tie between the betalain families and the Caryophyllaceae and Molluginaceae; confirms the exclusion of the Batidaceae, Gyrostemonaceae, and Theligonaceae from the Centrospermae; dismisses any close relationship between the Centrospermae and the Plumbaginaceae, Polygonaceae, or Primulaceae; eliminates the possibility of a close relationship among Plumbaginaceae, Polygonaceae, or Primulaceae; would not support a close relationship among the families in the Order Ranunculales; suggests that the Ranunculaceae may be the closest extant relative of the Centrospermae; supports separate family status for *Berberis* and *Mahonia*; indicates that most of the remaining berberidaceous genera are best treated as one family; should be regarded as a critical or key characteristic for determining the position in the dicot hierarchy of Batidaceae, Gyrostemonaceae, and Corynocarpaceae, and, to a lesser extent, Theligonaceae.

The present system for the classification of the angiosperms is based primarily on floral morphology, and most families have been the subject of detailed studies, reexaminations, and even revisions. Over the last few decades the relationships of various taxa have been refined and clarified by the incorporation of data from sources such as cytology and phytochemistry. The information derived from palynological investigations has also had a limited influence, but the development of the scanning electron microscope (SEM) has revolutionized the study of surface structures by providing a depth of focus never possible in light microscopy. Palynologists now have the means to fully exploit the morphological characteristics of the male gametophyte with the attendant conservatism and stability associated with reproductive structures. The potential influence of pollen morphology on the classification of the angiosperms cannot be overemphasized; for the first time there is a parameter which is ubiquitous, the material readily obtainable (the vast herbarium collections of the world) and simple to prepare, and the resulting micrographs have great precision and a degree of uniformity that permits accurate comparison regardless of their source.

While the flower may indeed be ubiquitous to the angiosperms, the great proliferation and modification of each of the parts make it nearly impossible to utilize the principle of comparative morphology (i.e., similarity indicates relationships) unless the taxa are already considered related (some major specializations in common), and the question is the extent of relationship to each other.

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In the last ten years the SEM has revealed an almost unbelievable diversity of pollen morphology, but this variation does not have the complexities of floral morphology and the associated difficulties of interpretation.

This paper reviews the results from an extensive and continuing investigation that had its origins in delimiting the order Centrospermae, perhaps the most distinctive order in the flowering plants. At this writing, the pollen of 650 species has been examined and the list now includes the Plumbaginales, Polygonales, Primulales, Ranunculales and Dilleniales. The authors hope to demonstrate the value of pollen morphology—the nature of evidence, the interpretation, the implications—in assessing the relationships of large taxa, mostly families, to each other.

The organization of this article is as follows: orders Centrospermae s.l., Plumbaginales, Polygonales, Primulales, Ranunculales, and Dilleniales. The families within each of these orders will be described with reference to size, distribution, unusual characteristics of floral and/or vegetative morphology, and problematical genera. An overview of the pollen morphology of each of these families is presented: aperture type, tectum, and wall structure, with the range of variation in each, and distinguishing features, if any. Finally, the relationships of each family as indicated by the palynological data.

All pollen has been processed for light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM) by methods already described (Nowicke & Skvarla, 1977). All specimens studied are listed in Table 1.

### THE ORDER CENTROSPERMAE

The order Centrospermae, which in the past has been circumscribed by a host of floral and embryological features, the most definitive being a curved embryo with a perisperm storage tissue, may well be the best example of a large natural association of families. The common morphological characteristics have, however, all been eclipsed by discoveries made at the chemical and ultrastructural levels.

Most of the red blue colors in the flowering plants are due to a general class of pigments, the water soluble anthocyanins, present in the cell vacuole. For the vast majority of the angiosperms the structure of the anthocyanin molecule varies only slightly. In the order Centrospermae, however, the molecule responsible for the red blue color is significantly altered by the incorporation of two (usually) nitrogen atoms. These N-containing pigments have been designated "betalains," after the genus in which they were first discovered, *Beta* L., in the Chenopodiaceae. The anthocyanins and the betalains never occur together in individual plants, different plants of a species, or families, etc.

The second discovery at the ultrastructural level was the existence of two types of sieve-tube plastids, starch or protein, with the former being the most common in the dicots. The Centrospermae have a unique protein type, a peripheral ring of fibrous protein and usually a central crystalloid (Behnke, 1976).

The discovery of the betacyanins and their gradual elucidation date back to the second half of the 19th century (see Dreiding, 1961, for review). The dean of American plant anatomists, Katherine Esau, appears to have been the

TABLE 1. Specimens examined, arranged alphabetically by family.

Taxa	Collector	Location	Figure	Pollen Description
				Aperture, Tectum
<b>ACHATOCARPACEAE</b>				
<i>Achatocarpus spinulosus</i> Grisebach	Venturi 472	Argentina	59	4-6-porate, coarsely granular
<b>AIZOACEAE (including Molluginaceae)</b>				
<i>Acrodon bellidifloris</i> N. E. Brown	Van der Bijl 33 (K)	S. Africa		3-colpate, spinulose-perforate
<i>Adenogramma galioides</i> Fenzl	Rogers, F. A. 16132	S. Africa		3-colpate, spinulose-punctate
<i>Aizoon hispanicum</i> L.	Kocher B-237	Jordan		3-colpate, spinulose-punctate
<i>Delosperma abyssinicum</i> Schwantes	Gillett 13948 (K)	E. Africa		3-colpate, spinulose-perforate
<i>D. ecklonis</i> Schwantes	Brown s.n. 1/29/22 (K)	Oxford Bot. Gards.	23	3-colpate, spinulose-perforate
<i>D. mahonii</i> N. E. Brown	Galpin 1085 (K)	S. Africa		3-colpate, spinulose-perforate
<i>Gisekia pharnaceoides</i> L.	Kundu & Balakrishnan 361	Ceylon	1, 2, 37	3-colpate, spinulose-punctate
<i>Macarthuria australis</i> Hueg.	Shell Oil Co. USNH 1756519	Australia		3-colpate, spinulose-punctate
<i>Pharnaceum incanum</i> L.	Rogers 16737	S. Africa	16	3-colpate, spinulose-punctate
<i>Sesuvium erectum</i> Correll	Stearns 33	Texas		3-colpate, spinulose-punctate
<i>S. maritimum</i> Britt., Sterns & Pogg.	Killip 40932	Florida		3-colpate, spinulose-punctate
<i>S. verrucosum</i> Raf.	Wooton & Standley s.n. 9/15/07	New Mexico		3-colpate, spinulose-punctate
<i>Tetragonia dimorphantha</i> Pax	Werdermann & Oberdieck 2292	S.W. Africa		3-colpate, spinulose-punctate
<i>T. pedunculata</i> Phil.	Metcalf 30339	Peru		3-colpate, spinulose-punctate
<i>T. vestita</i> I. M. Johnston	Hutchison 1320	Peru	3, 4, 38	3-colpate, spinulose-punctate
<b>AMARANTHACEAE</b>				
<i>Alternanthera flavescens</i> H.B.K.	Killip 42415a	Florida	36	recessed pores, spinulose-punctate
<i>Dicraurus leptocladus</i> Hook. f.	Pringle 13604	Mexico		recessed pores, spinulose-punctate
<i>Gomphrena brownii</i> Moq.	White, C. T. 8658	N. Queensland		recessed pores, spinulose-punctate
<i>G. elegans</i> Mart.	Ochoa 540	Peru	29, 49	recessed pores, spinulose-punctate
<i>Iresine angustifolia</i> Euphr.	Dugand 5486	Colombia	30, 52, 53	recessed pores, spinulose-punctate
<i>Pfaffia iresinoides</i> (H.B.K.) Spreng.	Bro. Daniel 741	Colombia	35	recessed pores, spinulose-punctate
<i>Tidestromia oblongifolia</i> (S.Wats.) Standl.	Train 662	California		recessed pores, spinulose-punctate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description
				Aperture, Tectum
<b>BASELLACEAE</b>				
<i>Basella excavata</i> S. Ell.	Croat 32007 (MO)	Madagascar	22, 54, 55	6-colpate, deeply punctate
<b>BATIDACEAE</b>				
<i>Batis maritima</i> L.	Gaumer & Sons 23257	Yucatan	61	3-colporoidate, finely granular
	Jack 7178	Cuba		3-colporoidate, finely granular
	McAtee 3287	Georgia	69, 70	3-colporoidate, finely granular
	Stoddart 440	British Honduras		3-colporoidate, finely granular
<b>BERBERIDACEAE</b>				
<i>Berberis fendleri</i> A. Gray	Eastwood 5272	Colorado	138, 144	irregular, unspecialized
<i>Diphylleia sinensis</i> Li	Rock 4230	China	140, 148	3-colpate, spinose
<i>Epimedium sempervirens</i> Nakai	Masayuki Oue 33	Japan	143	3-colpate, small rods randomly distributed
<i>Jeffersonia diphylla</i> (L.) Pers.	Shafer & Miller 180a	Pennsylvania	142, 147	3-colpate, striate
<i>Mahonia nervosa</i> (Pursh) Nutt.	Belton s.n. 5-26-43	Oregon	141, 145	irregular, unspecialized
<i>Podophyllum peltatum</i> L.	Braun 3911	Kentucky	146	3-colpate, small rods randomly distributed
	McDougall 1231	Mississippi	139	3-colpate, small rods randomly distributed
<b>CACTACEAE</b>				
<i>Opuntia lindheimeri</i> Engelm.	Griffiths 9031	Texas	21, 57	large pores, reticulate
<b>CARYOPHYLLACEAE</b>				
<i>Cometes surattensis</i> L.	Rechinger, K. H. & F. 3247	Iran	17, 45	3-colpate, spinulose-punctate
<i>Herniaria glabra</i> L.	Staszkievicz 527	Poland	24, 58	3 pores, spinulose-punctate
<i>H. hemistemon</i> J. Gay	Rechinger 8636	Iraq		pantoporate, spinulose-punctate
<i>Paronychia canadensis</i> (L.) Wood	Collins s.n. 7/12/31	Rhode Island		pantoporate, spinulose-punctate
	Fernald & Long 14325	Virginia		pantoporate, spinulose-punctate
<i>P. fastigiata</i> (Raf.) Fern.	Hartley & Peterson 7279	Wisconsin	31	pantoporate, spinulose-punctate
<i>Sclerocephalus arabicus</i> Boiss.	Mandaville 1251	Saudi Arabia	25	porate, spinulose-punctate
<i>Siphonychia americana</i> (Nutt.) T. & G.	Harper, R. 1696	Georgia		recessed pores, spinulose-punctate
	Thorne 15254	S. Florida	27, 50, 51	recessed pores, spinulose-punctate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description
				Aperture, Tectum
<i>S. diffusa</i> Chapm.	Wilbur & Webster 2660	Florida	26	recessed pores, spinulose-punctate
<i>S. pauciflora</i> Small	Brass 14469	Florida	33	recessed pores, spinulose-punctate
<i>S. rugelii</i> Chapm.	Thorne 6418	Georgia	32	recessed pores, spinulose-punctate
CHENOPODIACEAE				
<i>Anabasis setifera</i> Moq.	Mandaville, Jr. 3830	Saudi Arabia	28, 48	pantoporate, spinulose-punctate
<i>Beta vulgaris</i> L.	Bowden & Sims 1183	Balearic Islands	9, 10, 41, 42	pantoporate, spinulose-punctate
<i>Halocharis clavata</i> Bge.	Rechinger, K. H. 17312	Afghanistan		pantoporate, spinulose-punctate
<i>Nitrophila occidentalis</i> S. Wats.	Plumb 75	Arizona	34	pantoporate, spinulose-punctate
DIDIEREACEAE				
<i>Alluaudia humbertii</i> Choux	Decary s.n. 10/28/24	Madagascar	11, 12, 43	5-7 zonocolpate, spinulose-perforate
GYROSTEMONACEAE				
<i>Codonocarpus attenuatus</i> H. Walter	Vickery, J. s.n. 3-2-37	New South Wales	63	3-colpate, psilate
<i>C. cotinifolius</i> (Desf.) F. Muell.	Koch, M. 3021 (MO)	Merredin, W. A.	68	3-colpate, psilate
<i>Didymotheca pleiococca</i> F. Muell.	French, C. s.n. 1888	Australia	64	3-colpate, psilate
<i>Gyrostemon australasicus</i> (Moq.) Heimerl	von Mueller s.n. (MO)	Bordertown, S. A.	65, 66, 67	3-colpate, psilate
<i>Tersonia brevipes</i> Moq.	Muir 1125	Australia	62	3-colpate, psilate
<i>Tersonia brevipes</i> Moq.	Morrison s.n. 10/8/00	Australia		3-colpate, psilate
NYCTAGINACEAE				
<i>Boerhaavia erecta</i> L.	Harrison & Kearney 8016	Arizona	7, 8, 40	pantoporate, spinulose-tubuliferous
<i>Reichenbachia hirsuta</i> Spreng.	Elisa 3154	Paraguay	20, 56	3-colpate, reticulate
<i>Salpianthus arenarius</i> H. & B.	Purpus 6693	Mexico	14, 44	3-colpate, spinulose-punctate
PHYTOLACCACEAE				
<i>Phytolacca americana</i> L.	Larsen 779	Delaware	46	3-colpate, spinulose-punctate
	McGregor, E. 342	Kansas	15	3-colpate, spinulose-punctate
<i>Stegnosperma halimifolium</i> Benth.	Collins et al. 186	California	18, 47	3-colpate, spinulose-punctate
PLUMBAGINACEAE				
<i>Armeria maritima</i> (Miller) Willd.	Mathiesen & Pedersen s.n.	Denmark	85, 86	3-colpate, coarsely reticulate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description
				Aperture, Tectum
<i>A. maritima</i> var. <i>sibirica</i> (Turcz.) Lawrence	Svenson s.n.	Scandinavia	83, 84	3-colpate, finely reticulate
	Cody 1794	Greenland	77, 78, 79	3-colpate, reticulate
<i>Ceratostigma griffithii</i> C. B. Clarke	Calder 2014	Canada	80, 81, 82	3-colpate, reticulate
	Rock 6577	China	71, 72, 89	3-colpate, pointed verrucae
<i>Statice sinuata</i> L.	Rock 11578	China	73, 74, 90	3-colpate, rounded verrucae
	Maire & Wilczek 1048	Morocco	87	3-colpate, finely reticulate
	Vaccari 495	Greece	88	3-colpate, coarsely reticulate
<i>S. tenella</i> Turcz.	Chaney 517	Mongolia	75	3-colpate, coarsely reticulate
	Chaney 517a	Mongolia	76	3-colpate, finely reticulate
POLYGONACEAE				
<i>Atraphaxis spinosa</i> L.	Rechinger, K. H. 16625	Afghanistan	95, 96, 118, 119	3 colporate, striate-punctate
<i>Chorizanthe paniculata</i> Benth.	Bro. Claude Joseph 2997	Chile	97, 120	3 colporate-punctate
<i>Emex australis</i> Steinheil	Seydel 2975	S.W. Africa	98, 122, 123	3 colporate, spinulose-perforate
<i>Fagopyrum cymosum</i> (Trev.) Meisn.	Stainton, Sykes, Williams 630	Nepal	92	3 colporate, deeply punctate
<i>F. esculentum</i> Moench	Braun s.n.	Ohio	116	3 colporate, deeply punctate
<i>Koenigia islandica</i> L.	Eyerdam 1601	Alaska	93, 94, 117	pantoporate, spinulose
<i>Muehlenbeckia polybotryar</i> Meisn.	Pritzel 399	Australia	91, 115	3 colporate, punctate-striate
<i>Podopterus mexicanus</i> H. & B.	Langlassi 922	Mexico	100, 121	3 colporate, microreticulate
<i>Polygonum amphibium</i> L.	Braun s.n. VI-29-12	Indiana	105, 112	pantocolpate, finely reticulate
<i>P. cilinode</i> Michx.	Hardin 722	N. Carolina	107, 111	3 colporate, finely punctate-striate
<i>P. convolvulus</i> L.	Horr & McGregor E495	Kansas	103, 109	3 colporate, psilate and spinulose
<i>P. forrestii</i> Diels	Rock 9697	China	104, 110	pantocolpate, spinulose
<i>P. glaciale</i> (Meisn.) Hook. f.	Stainton et al. 3872	Nepal	106	3-colpate, reticulate
<i>P. orientale</i> L.	Johnston s.n. 8/16/24	New York	108, 113	pantoporate, reticulate
<i>P. vacciniifolium</i> Wall.	Koelz 976	India	101, 114	3 colporate, punctate
<i>Rumex scutatus</i> L.	Pfister 1158/2	France	99	3 colporate, spinulose-perforate
<i>Ruprechtia pallida</i> Standl.	Newman 17	Mexico	102, 124	3 colporate, perforate-rugulose

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description
				Aperture, Tectum
<b>PORTULACACEAE</b>				
<i>Anacampteros filamentosa</i> Sims	Rose & Stewart s.n. 1912	S. Africa		pantocolpate, spinulose-perforate
<i>Ceraria fruticulosa</i> Pears. & Steph.	Werdermann & Oberdieck 566	S.W. Africa	5, 6, 39	3 colporate, spinulose-punctate
<i>Lenzia chamaepitys</i> Phil.	Johnston 6091	Argentina	13	3-colpate, spinulose-punctate
<i>Montia meridensis</i> Friedr.	Hammen 1194	Colombia	19	pantocolpate, reticulate
<b>PRIMULACEAE</b>				
<i>Anagallis linifolia</i> L.	Reverchon 388	Spain	126, 133	3 colporate, prominently punctate
<i>Coris monspeliensis</i> L.	Tidestrom 13554	France	125, 131	3 colporate, sculptured and psilate
<i>Cortusa matthioli</i> L.	Koelz 4994	India	127, 135, 136	3 syncolporate, granular
<i>Glaux maritima</i> L.	Haakana s.n.	Finland	128, 132	3 colporate, punctate-striate
<i>Naumbergia thyrsoflora</i> (L.) Reichenbach	Andersen s.n.	Norway	129, 134	3 colporate, irregularly microreticulate
<i>Primula officinalis</i> (L.) Jacq.	Ludera s.n.	Poland	130, 137	5-8 zonocolpate, microreticulate
<b>RANUNCULACEAE</b>				
<i>Adonis pyrenaica</i> DC.	Salzmann s.n.	France	153, 158	3-colpate, spinulose-punctate
<i>Anemone coronaria</i> L.	Heldreich s.n. 12. 91.	Greece	149, 155	pantoporate, spinulose-punctate
<i>Clematis orientalis</i> L.	Raikova 2915	U.S.S.R.	152, 156	3-colpate, spinulose-punctate
<i>Coptis occidentalis</i> (Nutt.) T. & G.	Constance, Clements, Rollins 1065	Idaho	159	pantoporate, spinulose-punctate
<i>Eranthis hyemalis</i> (L.) Salisb.	Sandberg 217	Idaho	151	pantoporate, spinulose-punctate
	Javorka & Timko s.n. 3/1/11	Hungary	154	3-colpate, spinulose-punctate
<i>Helleborus viridis</i> L.	Livingston s.n. 27/3/66	England	164, 165	3-colpate, reticulate
<i>Paeonia brownii</i> Dougl.	Cronquist 6380	Oregon	160, 161	3-colpate, finely reticulate
<i>Ranunculus muricatus</i> L.	Koelz 14669	Iran	150, 157	pantocolpate, spinulose-punctate
<i>Trollius acaulis</i> Lindl.	Koelz 5046	India	162, 163	3-colpate, striate
<b>THELIGONACEAE</b>				
<i>Theligonum cynocrambe</i> L.	Pitard 263 (MO)	Tunesia	60	pantoporate, "reticulate"

first to detect the proteinaceous fibers in the sieve-tube plastids of *Beta vulgaris* L., in 1934. There is an apparent gap in the literature until 1964 when Falk reported this type in *Tetragonia expansa* Murr., from the Aizoaceae. But until examination of large numbers of taxa revealed the restricted distribution, the significance of these discoveries could not be fully appreciated (Behnke, 1975).

In fact, the extreme distinction of the order has been exploited by some phylogeneticists as evidence of a polyphyletic origin of the angiosperms. This may be overstating the case, but it would be difficult to refute the idea that the ancestral stock of the Centrospermae separated very early in time from the remaining angiosperms, certainly from the dicots. If the separation was later, then the large size of the order has been the result of rapid proliferation and this phenomenon is more difficult to explain.

Two families, the Caryophyllaceae and the Molluginaceae, which have been placed in the Centrospermae by various authors on morphological bases (Harms, 1934; Cronquist, 1968; Takhtajan, 1969), lack the distinctive betalain pigments. As a result, their placement has been the subject of some controversy.

When Behnke's (1969) investigations of sieve-tube plastids were extended to the Caryophyllaceae and Molluginaceae, he found that these two anthocyanin families had the peripheral ring of fibrous proteins that characterized the betalain families. Moreover, he was now able to distinguish three groups based on the central crystalloid: globular, the most common; polygonal, found in the Caryophyllaceae and in two other genera, *Limeum* (Molluginaceae) and *Stegnosperma* (Phytolaccaceae); and crystalloid-free, having only the ring, found in two families, the Amaranthaceae and the Chenopodiaceae.

In an effort to assess the degree of relationship between the anthocyanin families, Caryophyllaceae and Molluginaceae, to the betalain families, and to clarify the disputed relationships of four small families, Achatocarpaceae, Batidaceae, Gyrostemonaceae, Theligonaceae, to the Centrospermae, the pollen of 190 species from 16 families was examined (Nowicke, 1975). The significant result with the attendant conclusion was: the vast majority of the taxa examined in the betalain families, as well as the two anthocyanin families, Caryophyllaceae and Molluginaceae, had pollen grains with a very similar, sometimes indistinguishable morphology; and the two groups are very closely related to each other. Approximately 85% of the species examined had a tectum which could be described as spinulose and/or perforate, punctate, or tubuliferous. The pollen morphology of each of the four small families mentioned above does not support a relationship to the Centrospermae, nor to any of the remaining three for Achatocarpaceae or for Theligonaceae. The Batidaceae and Gyrostemonaceae have in common several unusual features, including the structure of the exine, and will be discussed in this paper.

The structure of the exine in the centrospermous families was the subject of a paper by Skvarla & Nowicke (1976), in which 33 genera from 11 families were examined in thin section. All 33 taxa had an exine organized into the foot layer, columellae, and tectum units considered typical for the angiosperms. With a few exceptions the endexine is poorly developed, sometimes apparently absent. Any noteworthy characteristics found in thin section in the 1976 study or in subsequent ones will be discussed under the particular family.



Sixteen families, Phytolaccaceae, Nyctaginaceae, Portulacaceae, Amaranthaceae, Chenopodiaceae (including Dysphaniaceae), Caryophyllaceae, Cactaceae, Aizoaceae, Molluginaceae, Basellaceae, Didiereaceae, Halophytaceae, Achato-carpaceae, Theligonaceae, Gyrostemonaceae, and Batidaceae will be discussed according to phylogenetic relationships where feasible; changes or implications brought out by subsequent investigations (Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977, 1979, etc.) will be included with the particular family.

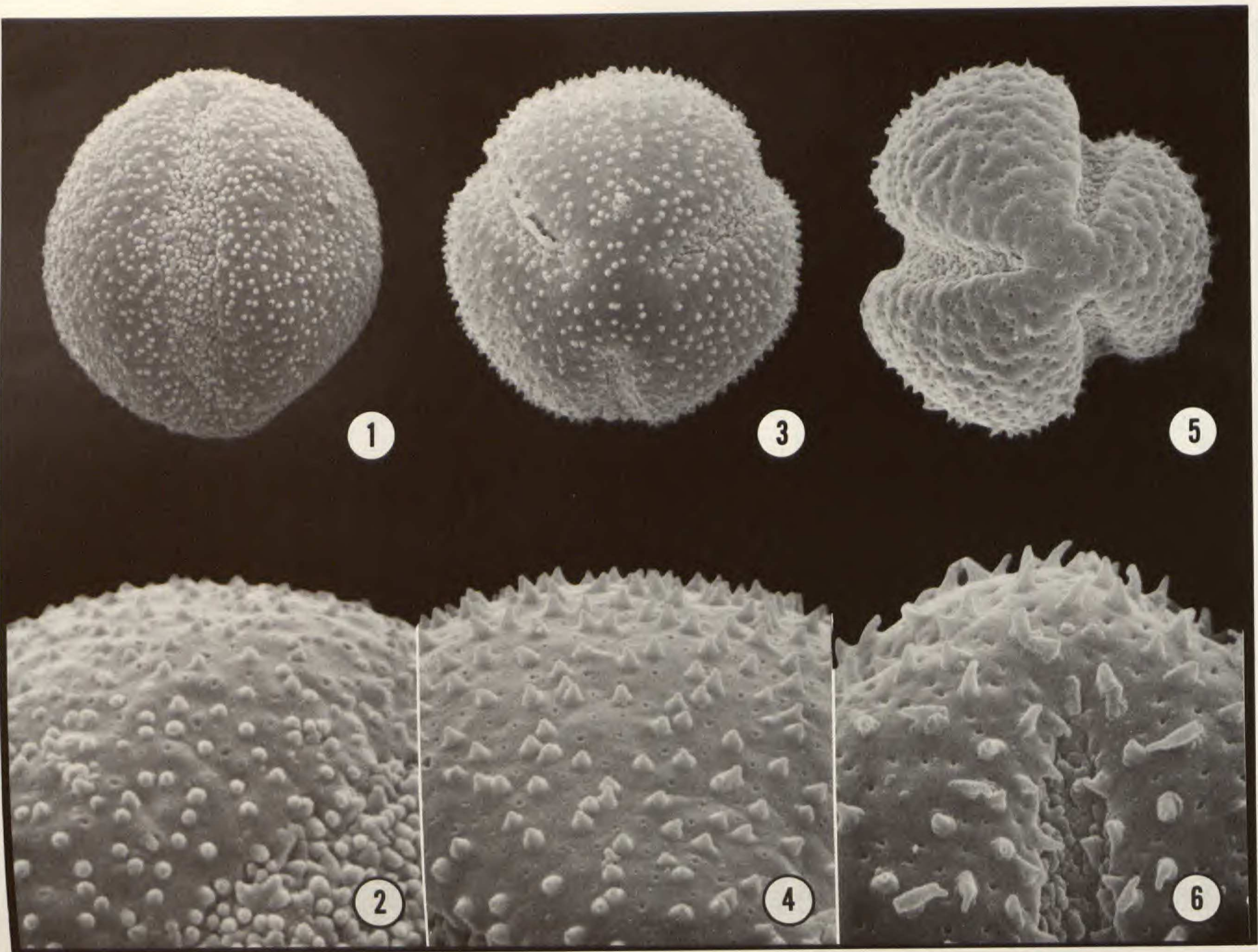
#### PHYTOLACCACEAE

The modern concept of the Phytolaccaceae includes 17 genera and perhaps as many as 80 species, distributed mostly in the warmer regions of the New World. The family has been considered as the most primitive in the order, and Buxbaum (1961) has referred to *Phytolacca* as the primordial genus, noting the similarity of the free carpelled species (sect. *Pircunia*, e.g., *P. acinosa*) to *Pereskia* (Cactaceae) and *Illicium*, a monotypic family in the Magnoliales. It might be more accurate to describe the family as unspecialized in view of the random variation in the floral parts: a calyx of four or five segments, usually dry and inconspicuous; the corolla absent; the stamens vary in number and placement within species, plants or even inflorescences; the position of the ovary, the carpel number, and the extent to which they are united can also vary within a species and within an inflorescence.

The pollen morphology has been thoroughly investigated by Bortenschlager (1973) and by Nowicke (1968). All taxa have the spinulose and punctate/perforate tectum and apertures that are 3-colpate, pantoporate, or pantocolpate. The six taxa illustrated in SEM by Nowicke (1975: figs. 1–6) are representative of the Phytolaccaceae. In this paper *Phytolacca americana* and *Stegnosperma halimifolium* are illustrated in SEM and in TEM, Figs. 15 and 46, and 18 and 47, respectively. The unspecialized exomorphology is reflected in the structure of the exine: Fig. 46, a section through the mesocolpus of *Phytolacca americana*, and Fig. 47, a section of a whole grain of *Stegnosperma halimifolium*, have the foot layer, columellae and tectum represented in a manner typical of the dicots. An accumulation of endexine in the region of the aperture is a common characteristic in the Phytolaccaceae (Fig. 47), the Centrospermae, and dicots in general. But, for the most part, the Centrospermae do not have a well-developed endexine in nonapertural regions; in Fig. 46, it is represented by the slightly less electron dense "layer" most evident at the far right. *Microtea paniculata* has pollen which is pantoporate (Nowicke, 1975: fig. 4) and in thin section (Skvarla & Nowicke, 1976: fig. 37) the thicker tectum and thinner foot layer are more similar to some Caryophyllaceae (Skvarla & Nowicke, 1976: fig. 46, *Dianthus barbatus*; Nowicke & Skvarla, 1977: fig. 23, *Gymnocarpos fruticosum*) than to any phytolaccaceous taxa sectioned thus far.

#### NYCTAGINACEAE

The Nyctaginaceae with 28–30 genera and perhaps 250 species is found mostly in the tropics and subtropics of the New World. This family has the widest range of variation in pollen morphology and the different types fall along tribal and subtribal lines as established by Heimerl in 1934. In earlier contributions, Now-



icke (1970: figs. 1–18), Nowicke & Luikart (1971: figs. 1–14, 16–19), Nowicke (1975: figs. 7–12, 78–79, 82, 85), Skvarla & Nowicke (1976: figs. 10, 30–34), and Nowicke & Skvarla (1977: figs. 18, 27), illustrated the different types in SEM and TEM.

The subtribe *Mirabileae* has pollen characterized by very large, spherical grains, ca. 100–180  $\mu\text{m}$  in diameter, numerous small pores, very thick walls, and a spinulose and tubuliferous and/or perforate tectum (at least some tubules appear to be collapsed spines). *Boerhaavia erecta*, Fig. 7–8, and 40, is representative of this group (see also Nowicke, 1975: figs. 12, 78). The greatly enhanced foot layer, Fig. 40, accounts for much of the thickness of the exine.

The subtribe *Abroniinae* with only *Abronia* (Nowicke & Skvarla, 1977: figs. 18, 27) and the subtribe *Bougainvilleinae* with only *Bougainvillea* (Nowicke, 1975: fig. 11; Skvarla & Nowicke, 1976: fig. 33) have 3(–4)-colpate grains with an incomplete tectum of a reticulate configuration with numerous free columellae in the lumina.

The subtribe *Phaeoptilinae* with only *Phaeoptilum* (Nowicke, 1975: fig. 10) has pantocolpate (4-4-4) grains with a spinulose and punctate tectum.

The tribe *Colignonieae* with only *Colignonia* (Nowicke & Luikart, 1971: figs. 1–4) has pantoporate grains with a spinulose and perforate tectum. But the pores are fewer and larger than in the subtribe *Mirabileae* and can be arranged 4-4-4, rarely 5-5-5; the spines not nearly so prominent.

The tribe *Boldoeae* (Nowicke & Luikart, 1971: figs. 5–10) has three genera, *Boldoa*, *Cryptocarpus* (Nowicke, 1975: fig. 7) and *Salpianthus*, illustrated here by *S. arenarius*, Figs. 14, 44, all of which are 3-colpate with a spinulose and perforate tectum.

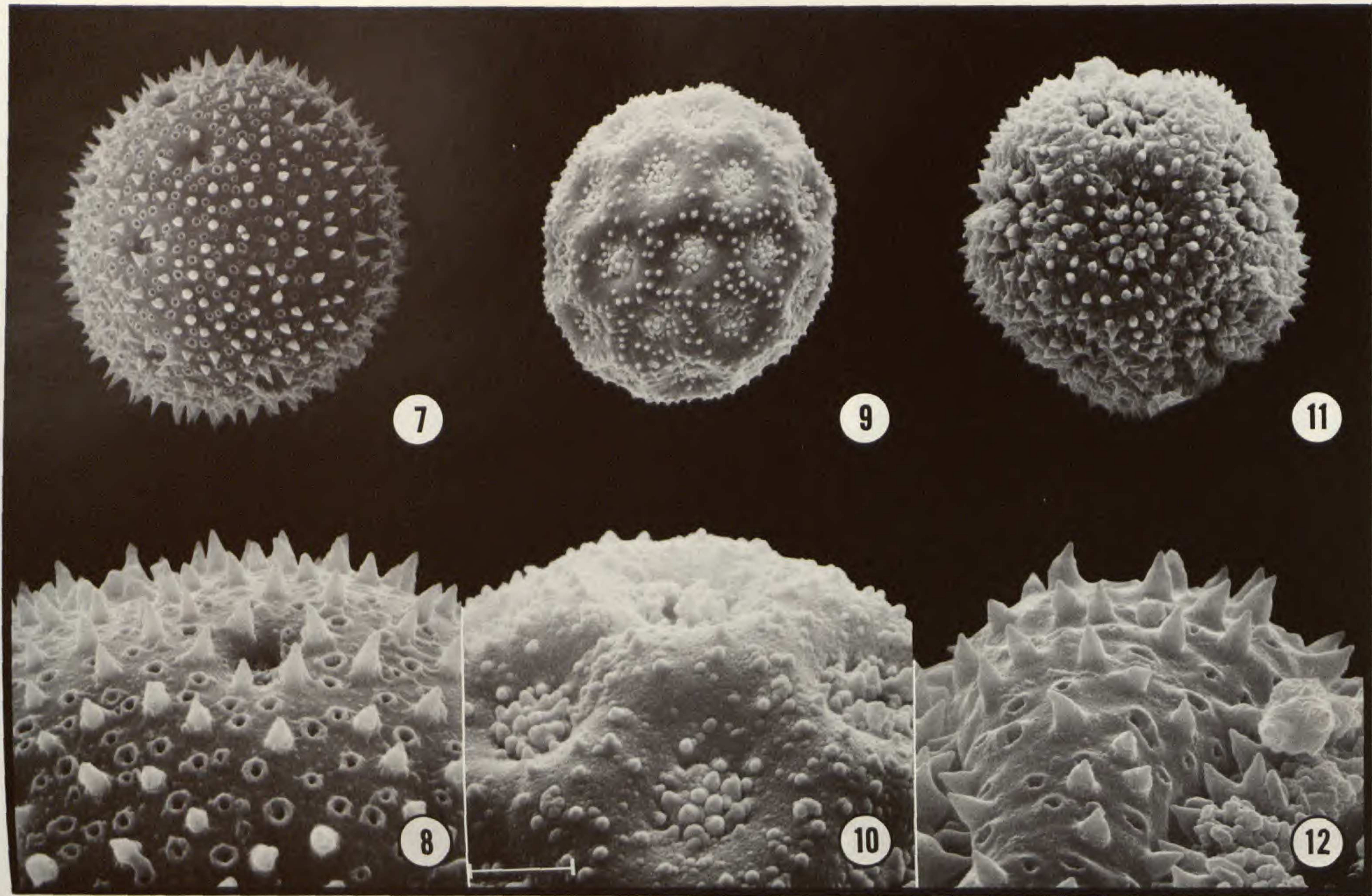
The TEM of *Salpianthus*, Fig. 44, is noteworthy for the following reasons: the foot layer is unusually thick and not an artifact since the presence of at least some continuous columellae indicates that the angle of section is only slightly oblique; the tectum is perforate and well developed; lastly, there is a thin, uniform endexine.

The tribe *Leucastereae* (Nowicke & Luikart, 1971: figs. 13–14, 16–19) has four genera, three of which, *Andradea* (fig. 17), *Leucaster* (fig. 16), and *Ramisia* (fig. 18) have 3-colpate grains with a spinulose and punctate tectum. *Reichenbachia hirsuta*, Figs. 20, 56, however, has an incomplete tectum of a reticulate configuration. The lumina are smaller than those found in *Abronia* and *Bougainvillea* and lack any free columellae. The most notable feature in thin section is the lamellar nature of the endexine.

The tribe *Pisonieae* has at least six genera, *Calpidia*, *Cephalotomandra*, *Neea*, *Pisonia*, *Pisoniella*, *Rockia*, that have 3-colpate, 6-pantocolpate, 12- or 15-pantocolpate (arranged 4-4-4, 5-5-5), rarely 18-pantocolpate (6-6-6) grains. More than one aperture type can be found in a species or in a sample. With the exception

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FIGURES 1–6. Scanning Electron Micrographs of Centrospermae pollen.—1. *Gisekia pharnaceoides* L. (Aizoaceae), equatorial view,  $\times 3,000$ .—2. *G. pharnaceoides*, ektexine surface,  $\times 7,900$ .—3. *Tetragonia vestita* I. M. Johnston (Aizoaceae), polar view,  $\times 1,900$ .—4. *T. vestita*, ektexine surface,  $\times 5,900$ .—5. *Ceraria fruticulosa* Pears. & Steph. (Portulacaceae), polar view,  $\times 1,900$ .—6. *C. fruticulosa*, ektexine surface,  $\times 5,900$ .



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of *Neea* (Nowicke, 1975: fig. 9), all taxa examined have a spinulose and punctate/perforate tectum (Nowicke, 1975: fig. 79). Some species of *Neea* have an incomplete tectum of a reticulate configuration but with smaller lumina than in *Abronia*, *Bougainvillea*, or *Reichenbachia*. The only member of this tribe examined in thin section is *Pisonia aculeata* (Skvarla & Nowicke, 1976: fig. 31). Some of the irregularity of the foot layer, stalactite-stalagmite appearance of the columellae, and thickened tectum are an artifact of the oblique angle of section.

#### PORTULACACEAE

For the Portulacaceae, a betalain family with as many as 350 species segregated into 19 genera, additional sampling has not revealed any unusual morphologies. Twenty-two species have been examined in these studies (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977), one of which, *Montia meridensis*, is illustrated in SEM for the first time in Fig. 19. The grain is 15-pantocolpate, the colpi arranged in a 5-5-5 pattern, and has an incomplete tectum which could also be described as finely reticulate. A paucity of material prevented examination in TEM or confirmation of the above, but there is no apparent reason to question the results. The pollen morphology of *Montiastrum* (Nowicke, 1975: fig. 18) is highly specialized and these grains could be distinguished from all other taxa examined in the Centrospermae and those in subsequent studies.

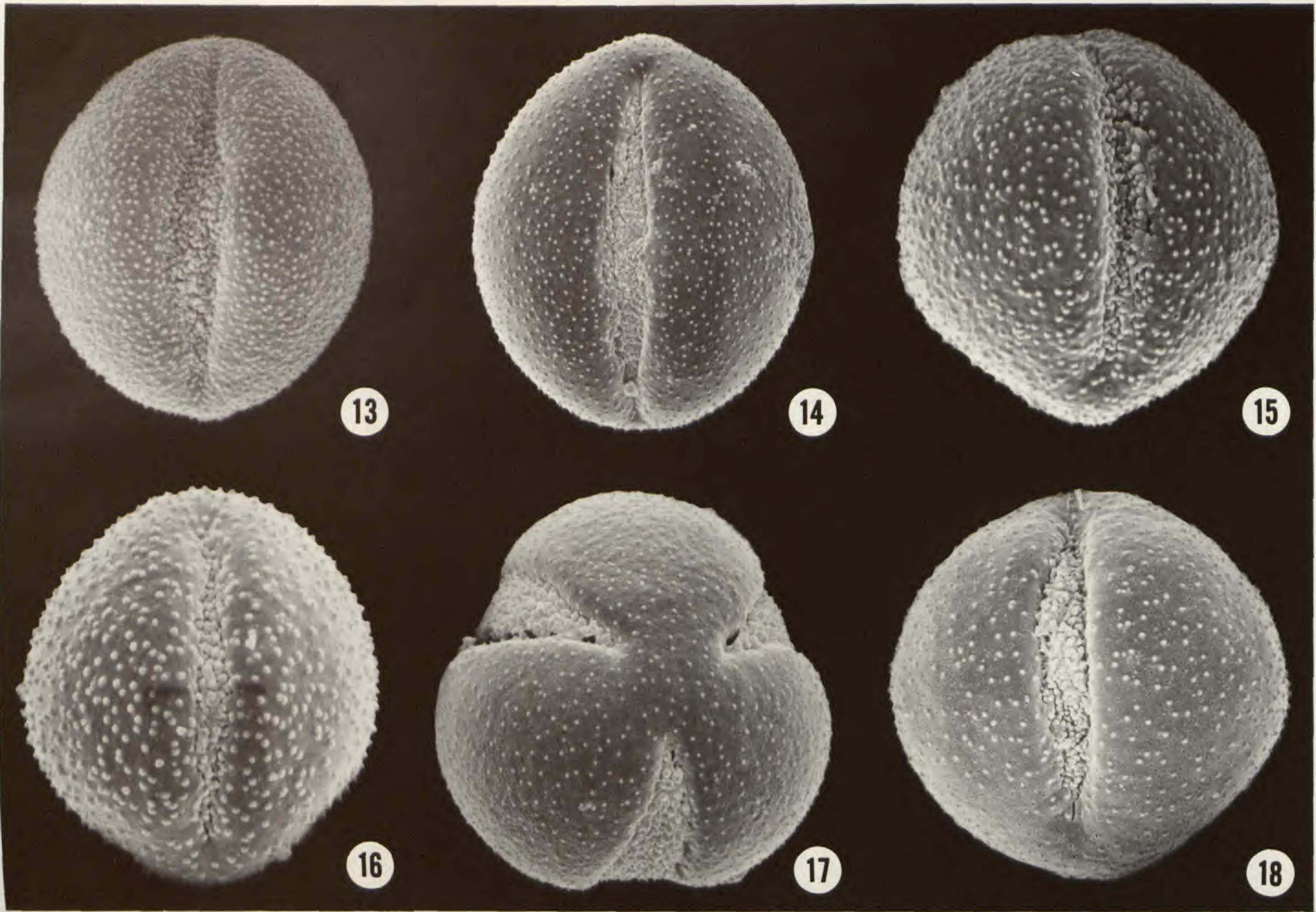
Twenty of the 22 species examined in the Portulacaceae have the spinulose and punctate/perforate tectum, differing mostly in the type of aperture: 3-colpate includes *Ceraria fruticulosa*, Figs. 5-6, and *Lenzia chamaepitys*, Fig. 13; pantocolpate includes *Talinum paniculatum* (Nowicke, 1975: fig. 16), *Portulaca grandiflora* (Nowicke, 1975: fig. 17), and *Naiocrene parvifolia* (Nowicke & Skvarla, 1977: figs. 6, 10, 28); pantoporate includes *Calandrinia ciliata* and *C. sericea* (Nowicke, 1975: fig. 15). The pollen of the last two species is very similar to some in the Cactaceae (Nowicke, 1975: figs. 19-20), Caryophyllaceae, Figs. 25, 31, and Chenopodiaceae, Figs. 28, 34: all have pores which are large in size, reduced in number, and symmetrically placed.

In TEM the exine of the Portulacaceae has a wider range of variation than most of the centrospermous families. Figure 39, *Ceraria fruticulosa*, illustrates a fragmented endexine, an irregular foot layer, variable columellae, and a well-developed tectum. At least part of the irregularity is the result of the slightly oblique angle of the section.

The exine structure of *Portulacaria afra* (Skvarla & Nowicke, 1976: fig. 39) is very similar to that of *Ceraria fruticulosa*, Fig. 39. *Calyptidium umbellatum* (Skvarla & Nowicke, 1976: fig. 38) and *Naiocrene parvifolia* (Nowicke & Skvarla, 1977: fig. 28) have a uniform foot layer, columellae which are regular in shape and distribution, and a tectum which is consistent with that depicted in SEM (Nowicke, 1975: fig. 14; Nowicke & Skvarla, 1977: figs. 6, 10). The exine of

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FIGURES 7-12. Scanning Electron Micrographs of Centrospermae pollen.—7. *Boerhaavia erecta* L. (Nyctaginaceae),  $\times 890$ .—8. *B. erecta*, ektexine surface,  $\times 2,300$ .—9. *Beta vulgaris* L. (Chenopodiaceae),  $\times 2,980$ .—10. *B. vulgaris*, ektexine surface,  $\times 7,700$ .—11. *Alluaudia humbertii* Choux (Didiereaceae),  $\times 920$ .—12. *A. humbertii*, ektexine surface,  $\times 3,850$ .



*Portulaca grandiflora* (Skvarla & Nowicke, 1976: fig. 40) is distinguished by the very thin foot layer, short, thick and sparsely distributed columellae supporting a thin tectum with prominent spines (Nowicke, 1975: fig. 81).

Unfortunately, the number of species examined in the Portulacaceae is insufficient to test McNeill's (1974) revised classification, but at this time it seems unlikely that pollen morphology will be a critical or key characteristic at any level. McNeill's (p. 726) first couplet for the key to tribes includes "pollen poly (30)-pantocolpate" versus "pollen various, very rarely polypantocolpate." At that time the pantocolpate characteristic was applicable only to *Portulaca*. But pollen studies since 1974 have reported this condition in species identified as belonging to *Anacampseros* (unpublished data), *Montia meridensis*, Fig. 19, *Naiocrene* (Nowicke & Skvarla, 1977: fig. 10), and *Talinum* (Nowicke, 1975: fig. 16). The apparent lack of agreement does not necessarily question McNeill's concept of the infra-familial classification, but may indicate that the palynological data have limited value at that level. All available evidence from pollen morphology does confirm the close relationship of the Portulacaceae to the betalain families and the Caryophyllaceae and Molluginaceae.

#### AMARANTHACEAE AND CHENOPODIACEAE

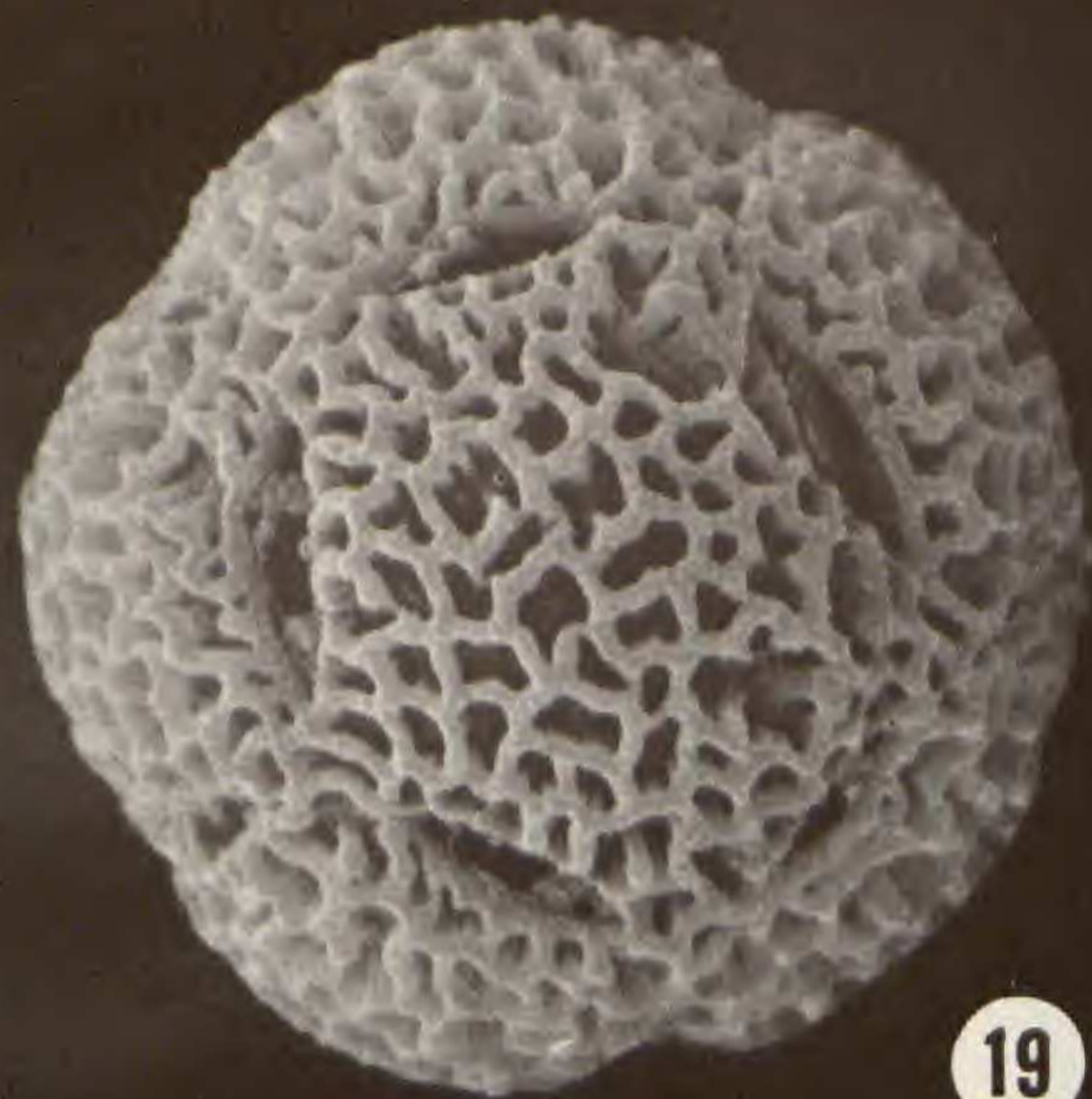
The Amaranthaceae and Chenopodiaceae have long been considered as closely related families: congested inflorescences with small, reduced flowers, the unilocular, 2–3-carpelled ovary, etc. The Chenopodiaceae is the larger family, with about 100 genera and 1,400 species, many with adaptations for physiologically dry habitats in temperate regions; the Amaranthaceae, with 64 genera and 800 species, is most abundant in tropical and subtropical regions.

Their close affinity to each other is reinforced by the peculiar variant of the protein of the sieve-tube plastid, which has only the peripheral ring of fibrous protein (Behnke, 1976: figs. 10, 12c, 13). The central crystalloid protein, found in all remaining betalain families and the Caryophyllaceae and Molluginaceae, is absent. The pollen morphology of the Chenopodiaceae and Amaranthaceae is also unusual: all taxa have grains which are pantoporate (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977). It is the negative aspect of this distribution that is perplexing: the absence of the basic 3-colpate type, especially in a family as large as Chenopodiaceae, could indicate that the ancestral branch which gave rise to these two families was, at that time, a constricted one.

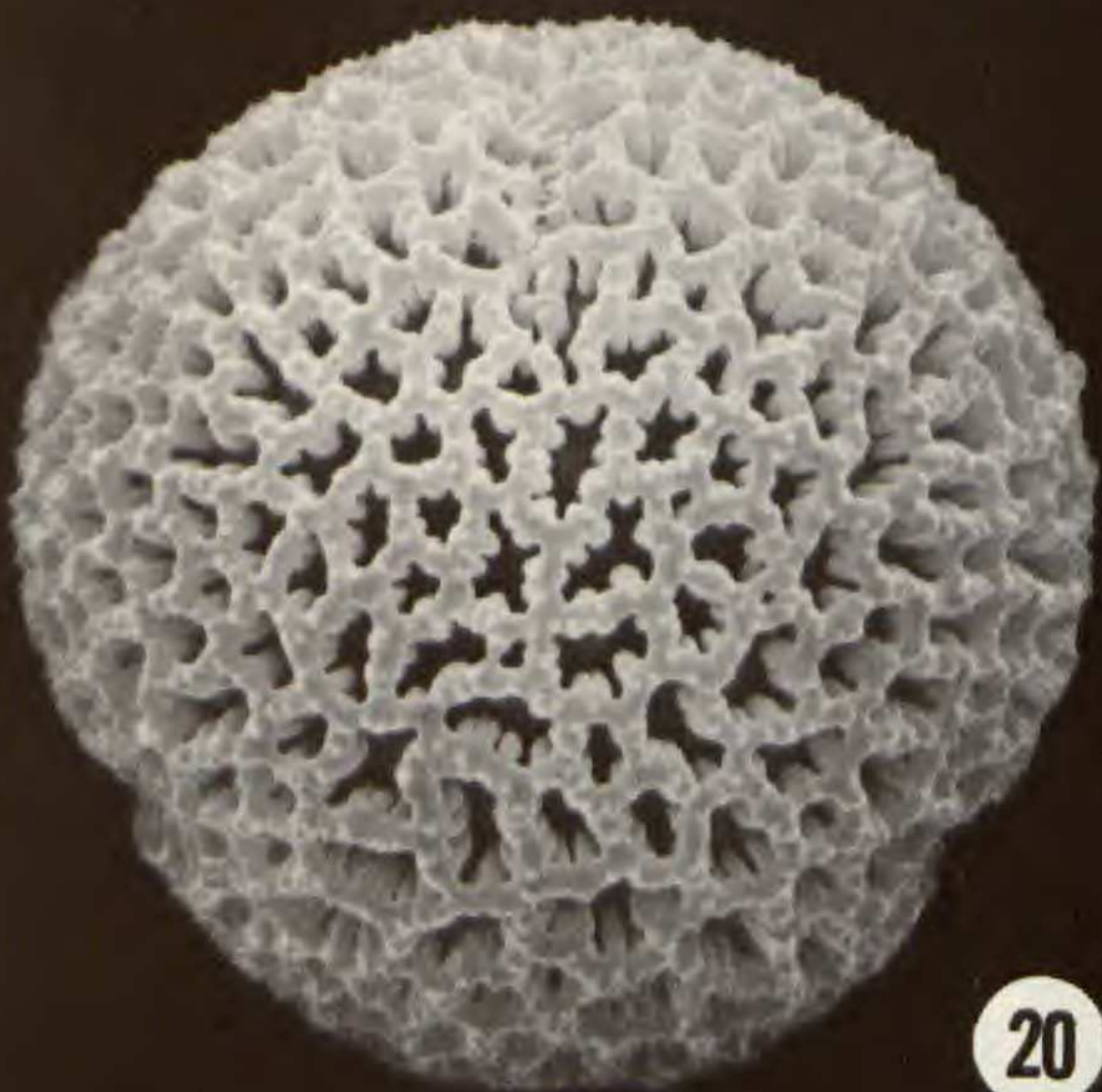
The Amaranthaceae and the Chenopodiaceae have the spinulose and punctate tectum but the perforations are very small and sparsely distributed, and in fact best illustrated in thin section, Figs. 41–42, 48, 52 (Skvarla & Nowicke, 1976: figs. 14, 23–27; Nowicke & Skvarla, 1977: figs. 20, 25), as opposed to SEM, Figs. 9–10, 28–30, and 34–36.

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FIGURES 13–18. Scanning Electron Micrographs of Centrospermae pollen.—13. *Lenzia chamaepitys* Phil. (Portulacaceae), equatorial view,  $\times 1,620$ .—14. *Salpianthus arenarius* H. & B. (Nyctaginaceae), equatorial view,  $\times 1,930$ .—15. *Phytolacca americana* L. (Phytolaccaceae), equatorial view,  $\times 2,430$ .—16. *Pharnaceum incanum* L. (Aizoaceae), equatorial view,  $\times 3,230$ .—17. *Cometes surattensis* L. (Caryophyllaceae), polar view,  $\times 1,850$ .—18. *Stegnosperma halimifolium* Benth. (Phytolaccaceae), equatorial view,  $\times 1,770$ .



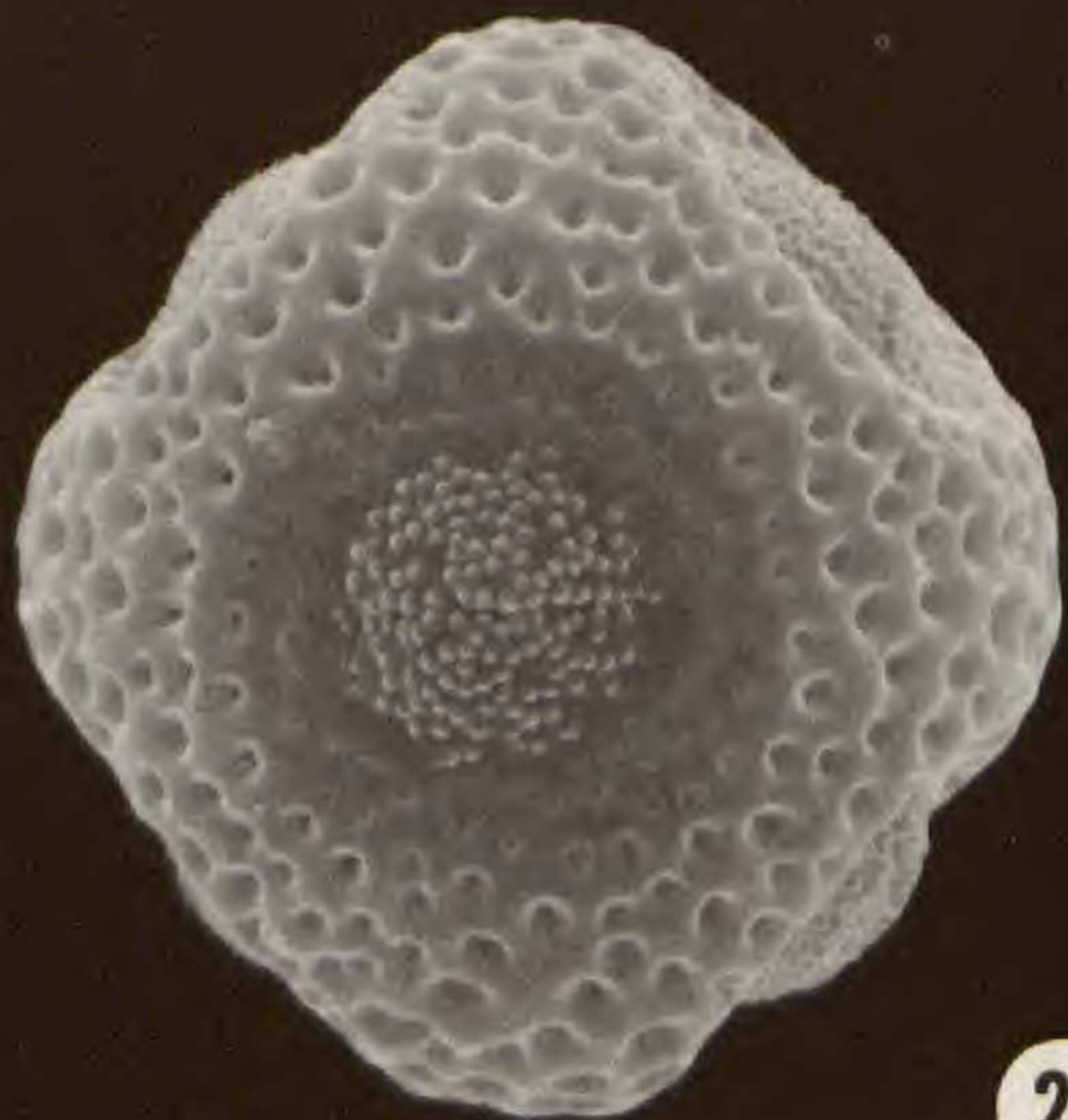
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The Amaranthaceae is divided into two subfamilies, Amaranthoideae and Gomphrenoideae, based on anther locules, 4 versus 2, respectively, and the ovary with one to many ovules versus always one ovule.

Within the taxa examined, the pollen of the Amaranthoideae can have pores which are small, numerous, not sunken, e.g., *Amaranthus* (Nowicke, 1975: fig. 56); or, larger and fewer pores, slightly recessed, e.g., *Aerva* (Nowicke, 1975: fig. 58), *Marcelliopsis* (Nowicke, 1975: fig. 57).

An unusual characteristic is found in some taxa in the Amaranthoideae: aperture plates that have four, five, or six identically shaped, recurved spines that produce a starlike structure. This condition is illustrated in *Pupalia lappacea* (Nowicke, 1975: fig. 59), and *Psilotrichum amplum* (Nowicke & Skvarla, 1977: figs. 13, 20). It is also present to varying degrees in *Aerva* (Townsend, 1974), *Centemopsis*, and *Robynsiella* (Livingstone et al., 1973).

The pollen in the subfamily Gomphrenoideae can be distinguished from that found in the Amaranthoideae or in the Chenopodiaceae by pores which are recessed, are separated by one, rarely two rows of columellae, and are either large and few in number, or small and more numerous. In each case apertures cover the surface of the grain. Those taxa with large pores include: *Alternanthera flavescens*, Fig. 36, *Gomphrena elegans*, Fig. 29, *Iresine angustifolia*, Fig. 30, *Pfaffia iresinoides*, Fig. 35, and *Tidestromia lanuginosa* (Nowicke, 1975: fig. 52). In *Brayulinea* (Nowicke, 1975: fig. 50) and particularly *Froelichia* (Skvarla & Nowicke, 1976: figs. 6, 10) the pores are smaller and more numerous. Whether each of the pores depicted in those taxa could function in germination is questionable, as is the adaptive value of numerous pores, or the selective pressures which could be responsible.

Thin section verifies the minimal separation of the pores in the *Gomphrena* types: Fig. 49, *Gomphrena elegans*, is a radial section parallel to the long axis of one murus (left), through the pore, slightly oblique to the long axis of the next murus. In an earlier study (Skvarla & Nowicke, 1976: figs. 16–18) the structure of the exine in *Gomphrena elegans* was clarified by three separate thin sections: parallel with a murus (fig. 16), through a sunken aperture in which the membrane is covered with flecks of ectexine (fig. 18), and a tangential section (fig. 17) illustrating the uniseriate row of columellae separating adjacent pores. The TEMs of *Iresine angustifolia*, a slightly oblique section through the murus in Fig. 52, and through the aperture in Fig. 53, agree with the surface morphology illustrated in SEM, Fig. 30.

The Chenopodiaceae, although a much larger family than Amaranthaceae, does not have a counterpart to the *Gomphrena* type. It does have taxa whose pollen closely resembles that of *Amaranthus*, i.e., numerous small pores, e.g.,

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FIGURES 19–24. Scanning Electron Micrographs of Centrospermae pollen.—19. *Montia meridensis* Friedr. (Portulacaceae), polar view, pantocolpate,  $\times 1,480$ .—20. *Reichenbachia hirsuta* Spreng. (Nyctaginaceae), oblique polar view, 3-colpate,  $\times 2,740$ .—21. *Opuntia lindheimeri* Engelm. (Cactaceae),  $\times 640$ .—22. *Basella excavata* S. Ell. (Basellaceae),  $\times 2,740$ .—23. *Delosperma ecklonis* Schwantes (Aizoaceae), oblique polar view,  $\times 4,030$ .—24. *Herniaria glabra* L. (Caryophyllaceae), equatorial view with prominent mesocolpial ridge,  $\times 4,180$ .



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*Beta vulgaris*, Figs. 9–10, *Chenopodium* (Nowicke & Skvarla, 1977: figs. 5, 25), *Grayia* (Nowicke, 1975: fig. 43), and *Borsczowia* (Nowicke, 1975: fig. 45).

A second pollen morphology found in *Anabasis setifera*, Fig. 28, *Halocharis* (unpublished data), *Nitrophila occidentalis*, Fig. 34, and *Traganum* (Nowicke, 1975: fig. 46), is distinguished by fewer, larger, slightly sunken pores, characteristics which, in combination, produce a polyhedrallike shape. Although similar to *Aerva* and *Marcelliopsis* (see above discussion) of the Amaranthaceae, the closest counterparts of these chenopodiaceous taxa are in the Caryophyllaceae: *Cerastium* (Nowicke, 1975: fig. 32), *Paronychia fastigiata*, Fig. 31, *P. canadensis* (unpublished data), *Sclerocephalus arabicus*, Fig. 25, *Scleranthus perennis* (Nowicke, 1975: fig. 31), and *Gymnocarpos* (Nowicke & Skvarla, 1977: fig. 4).

The Chenopodiaceae have an exine structure that could be characterized by Fig. 48, a radial section of *Anabasis setifera*: a thick, sparsely perforate tectum supported by prominent columellae which rest on a relatively thin foot layer (see also Skvarla & Nowicke, 1976: figs. 22–27). Within the Centrospermae this family had the most consistent presence of endexine (Skvarla & Nowicke, 1976: figs. 26–27). Figure 41 of *Beta vulgaris* is a section parallel with the mesoporal ridge; Fig. 42 is a radial section that cuts across two pores and at a right angle to the mesoporal ridge, illustrating the convex structure. The type of pollen morphology found in *Dysphania* (Nowicke, 1975: fig. 60) would support its inclusion in the Chenopodiaceae, as would the plastid subtype (Behnke & Turner, 1971) which lacks the central crystalloid.

#### CARYOPHYLLACEAE

The systematic significance of the pollen morphology of the Caryophyllaceae was the thrust of the original investigation, "Pollen Morphology in the Order Centrospermae" (Nowicke, 1975), and the irrefutable conclusion, documented by an extensive series of SEM micrographs (Nowicke, 1975: figs. 25–36, 74, 76, 84, 86, 88–89), was that, palynologically, the Caryophyllaceae are very closely related to the betalain families. Twenty-eight of the 33 species examined in that study had the spinulose and punctate/perforate tectum, 25 of the 33 were pantoporate, the remaining 8 were 3-colpate. Four collections variously identified as belonging to *Lychnis* (Nowicke, 1975: figs. 35–36, 84, 88), *Silene* (Nowicke, 1975: figs. 29–30, 89), or *Melandrium* (Skvarla & Nowicke, 1976: figs. 5, 12, 45) had a tectum in which the perforations were sufficiently large to be described as "reticulate," but the decision was and is an arbitrary one. Pantocolpate forms have been reported by other workers (Erdtman, 1966; Vishnu-Mittre & Gupta, 1964), but this condition has not been found in any of the species examined since the first study.

Figures 13 through 18 illustrate the similarity of the 3-colpate, spinulose/punc-

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FIGURES 25–30. Scanning Electron Micrographs of Amaranthaceae, Caryophyllaceae, and Chenopodiaceae pollen.—25. *Sclerocephalus arabicus* Boiss. (Caryophyllaceae),  $\times 2,810$ .—26. *Siphonochia diffusa* Chapm. (Caryophyllaceae),  $\times 3,190$ .—27. *S. americana* (Nutt.) T. & G.,  $\times 3,310$ .—28. *Anabasis setifera* Moq. (Chenopodiaceae),  $\times 4,100$ .—29. *Gomphrena elegans* Mart. (Amaranthaceae),  $\times 3,900$ .—30. *Iresine angustifolia* Euphr. (Amaranthaceae),  $\times 3,750$ .



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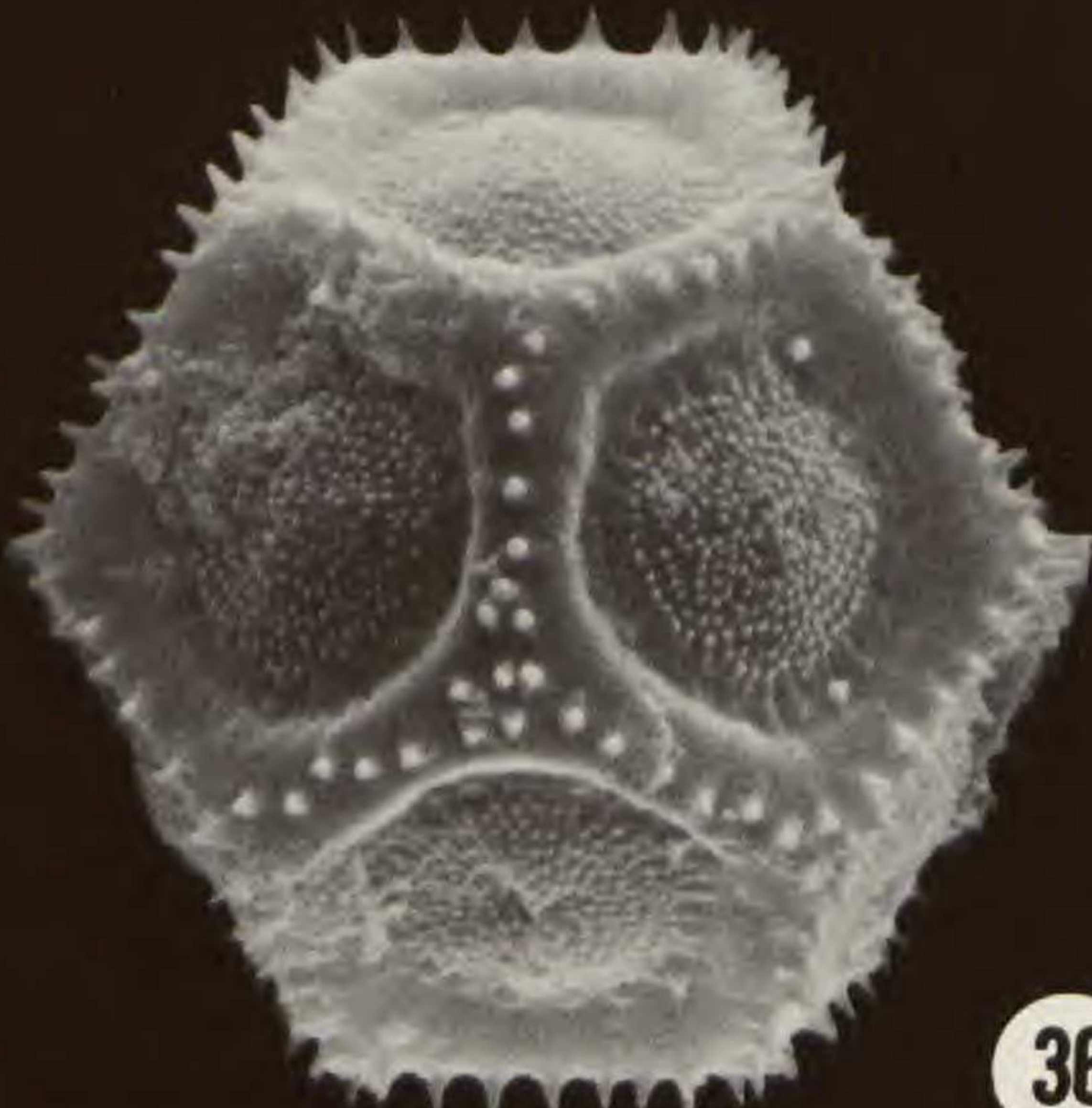
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tate pollen type in the Centrospermae, and as such confirm the close relationship of the families represented: Fig. 13, *Lenzia chamaepitys*, Fig. 14, *Salpianthus arenarius*, Fig. 15, *Phytolacca americana*, Fig. 16, *Pharnaceum incanum*, Fig. 17, *Cometes surattensis*, and Fig. 18, *Stegnosperma halimifolium*.

The structure of the exine in thin section, e.g., *Cometes surattensis*, Fig. 45, and *Corrigiola* (Skvarla & Nowicke, 1976: fig. 42) closely resembles that of the betalain families, e.g., Fig. 44, *Salpianthus arenarius*, Fig. 46, *Phytolacca americana*, Fig. 47, *Stegnosperma halimifolium*, and Fig. 54, *Basella excavata*.

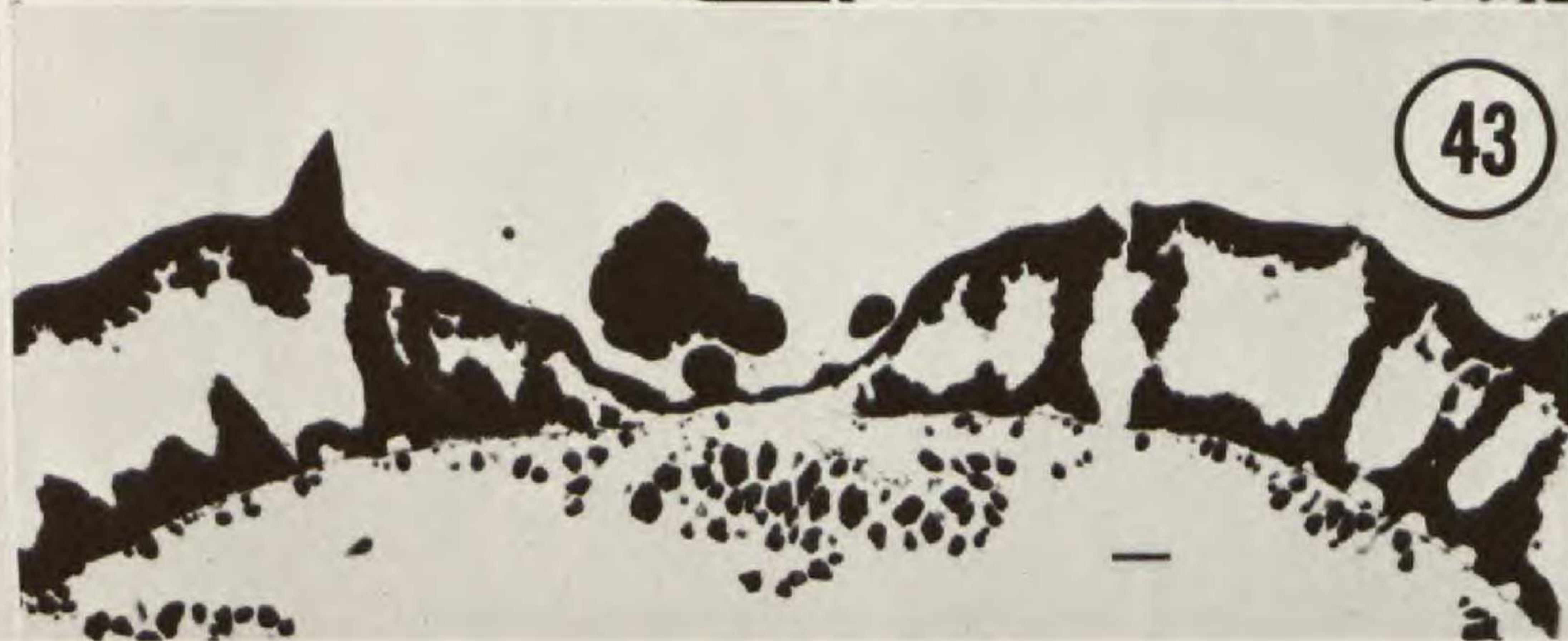
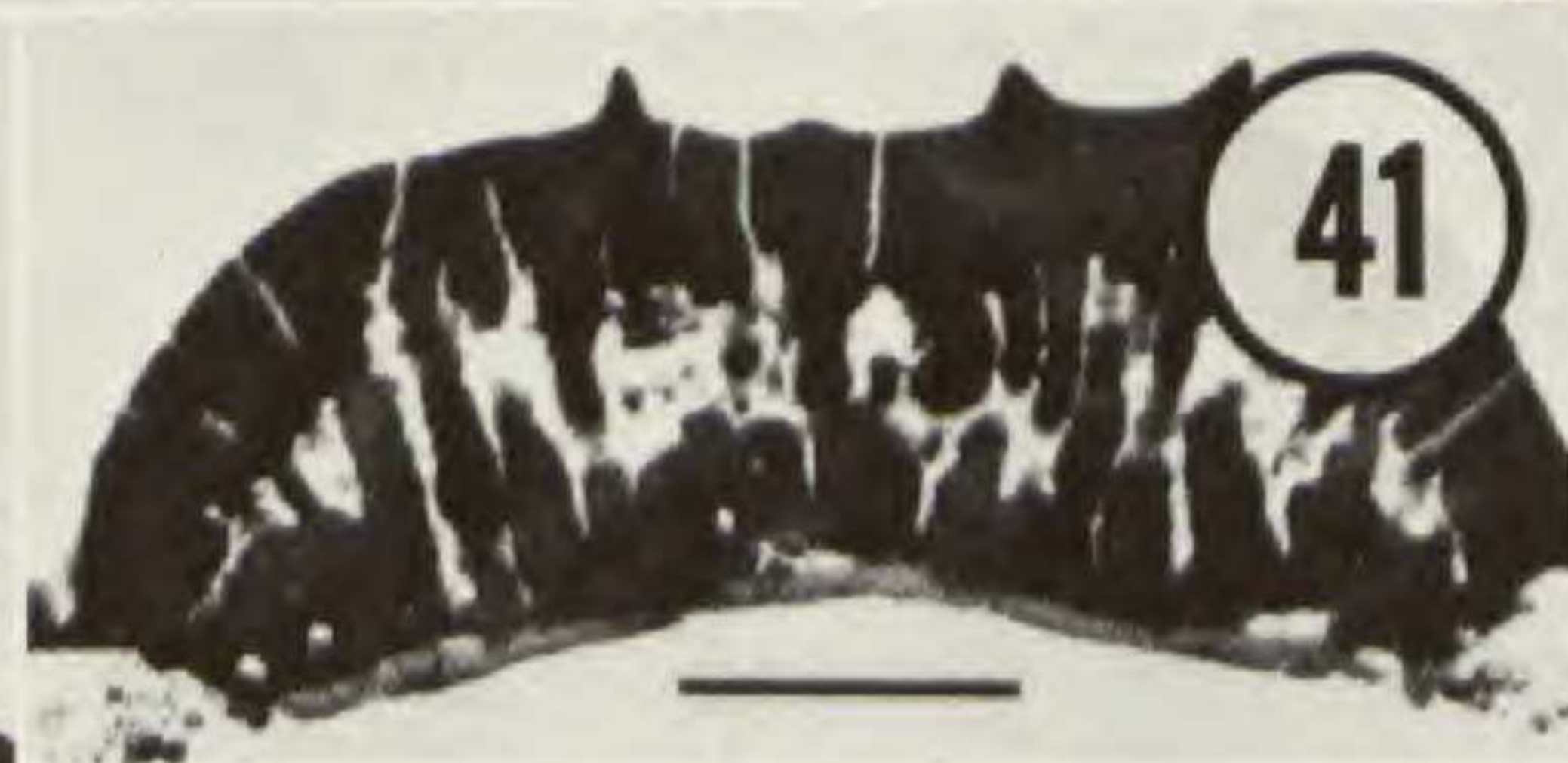
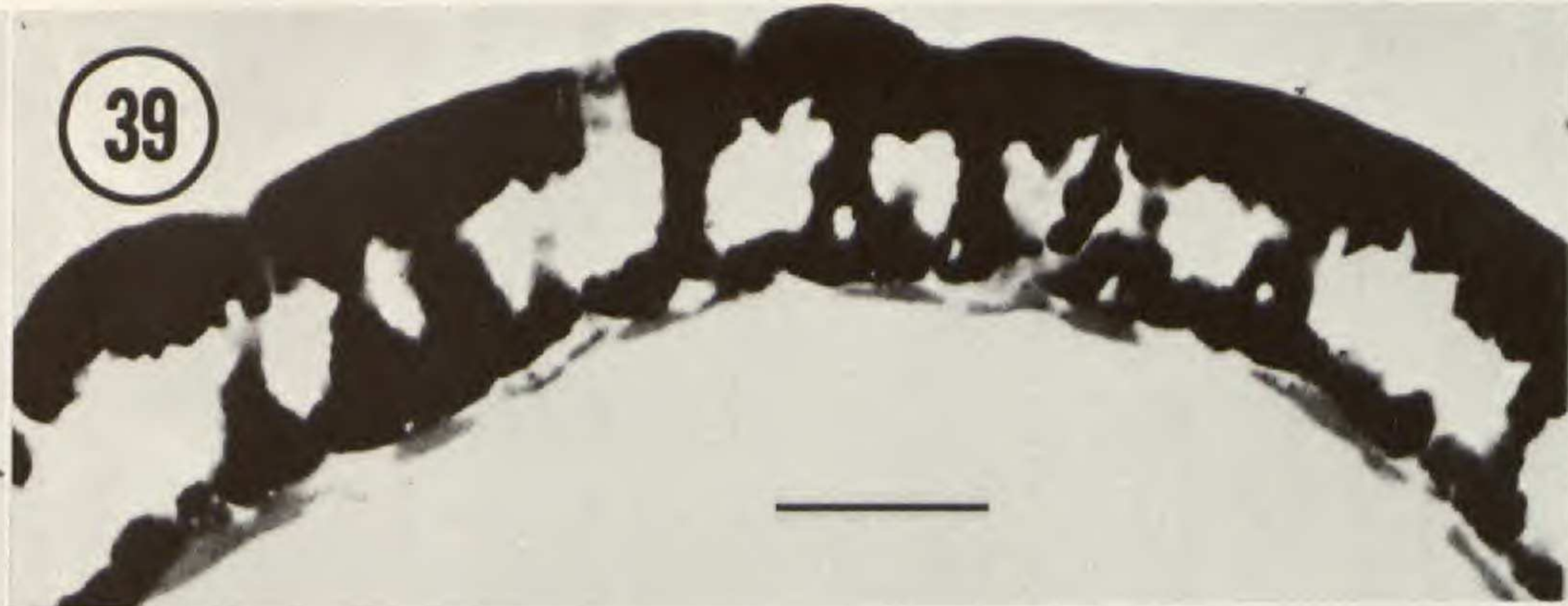
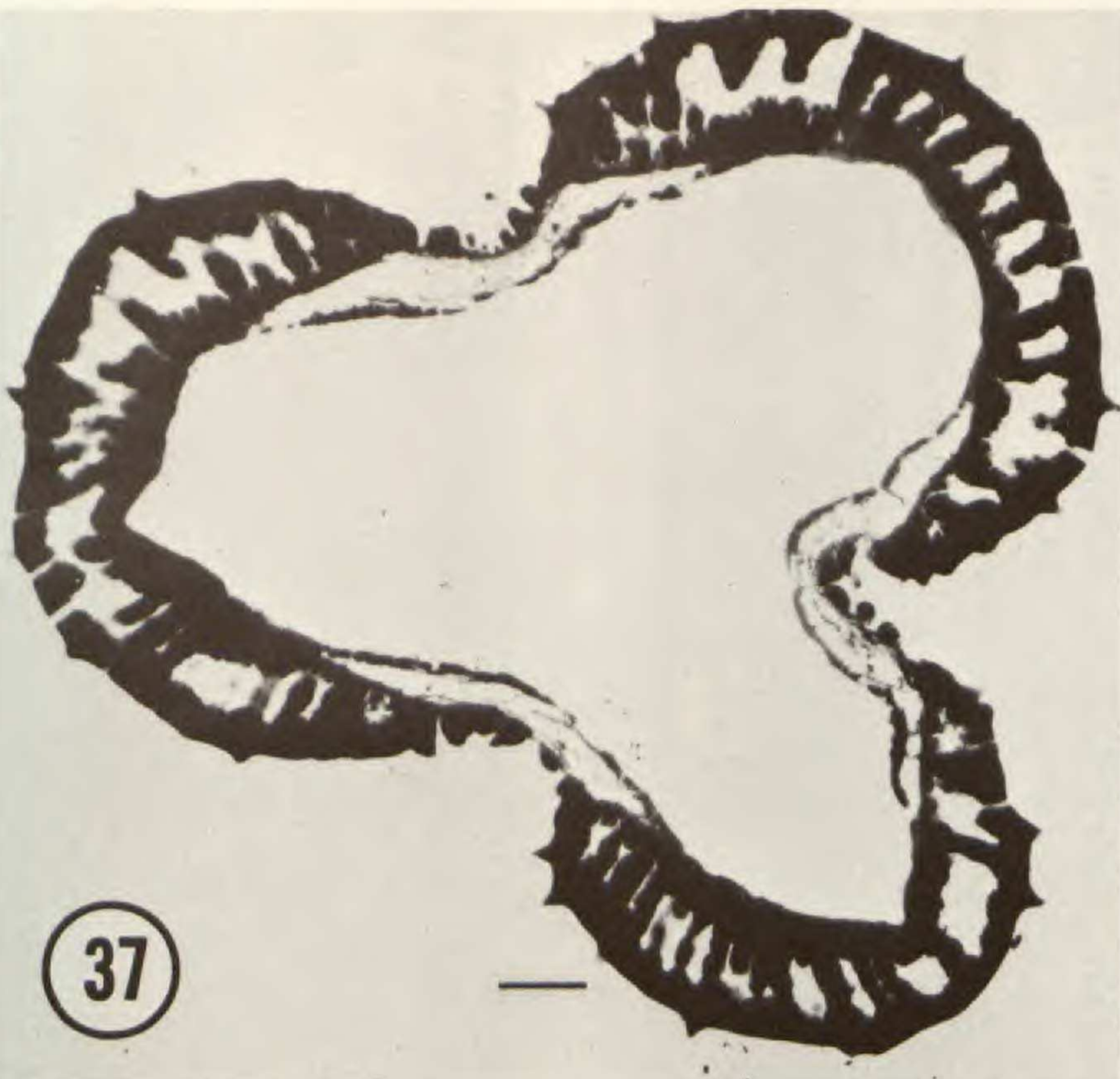
Figure 24, a whole grain, equatorial view of *Herniaria glabra*, is unusual in the presence of three large, poorly defined aperture areas, separated by a prominent mesocolpial ridge. There is a resemblance to the *Polygonum convolvulus* morphology in Fig. 103. However, the *P. convolvulus* type represents a complex morphology in which the two types of surface tectum are sharply demarcated from each other, and there is a zonorate endoaperture which is conspicuous in LM due to the thickened margins. Thin section of *H. glabra*, Fig. 58, illustrates an aperture with part of the mesocolpial ridge on each side. This structural organization contrasts sharply with the section of *P. convolvulus*, Fig. 109, in which, among other differences, the two apertures are underlain by a prominent endexine. This morphology is a fairly common one in the Polygonaceae and includes those taxa usually assigned to the genus *Polygonella* as well. *Illecebrum verticillatum* is the only other species in the Caryophyllaceae with a morphology similar to that in Fig. 24. *Herniaria hemistemon* and *H. hirsuta* (unpublished data) have pantoporate, spherical grains.

There have been any number of perplexing and unexpected results in these pollen studies: the structure of the exine in Batidaceae and Gyrostemonaceae; the magnitude of the distinction between the Armeria type and the Plumbago type in the Plumbaginaceae (Nowicke & Skvarla, 1977); the compacted columellae found in the *Bistorta* complex of *Polygonum* (Nowicke & Skvarla, 1977); and the close similarity in SEM of the Ranunculaceae and Centrospermae pollen are but a few. The most recent of these concerns the relationships of the Caryophyllaceae.

The placement of the Caryophyllaceae in the dicot hierarchy seems to reflect the nature of the latest discovery. Classical morphology allied the family with the Centrospermae. The presence of the anthocyanins as opposed to betacyanins seemed to dismiss the possibility of including the family in the Centrospermae (an opinion formerly held by the first author): Behnke's work on sieve-tube plastids (Behnke, 1976), the presence of a very distinctive type found only in the betalain families and Caryophyllaceae and Molluginaceae as well, created doubt, the more so the larger his sample size became. Neither author would be so presumptuous as to regard the recent results in the Caryophyllaceae as being

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FIGURES 31-36. Scanning Electron Micrographs of Amaranthaceae, Caryophyllaceae, and Chenopodiaceae pollen.—31. *Paronychia fastigiata* (Raf.) Fern. (Caryophyllaceae),  $\times 3,260$ .—32. *Siphonychia rugelii* Chapm. (Caryophyllaceae),  $\times 2,820$ .—33. *S. pauciflora* Small,  $\times 3,330$ .—34. *Nitrophila occidentalis* S. Wats. (Chenopodiaceae),  $\times 2,940$ .—35. *Pfaffia iresinoides* (H.B.K.) Spreng. (Amaranthaceae),  $\times 3,300$ .—36. *Alternanthera flavescens* H.B.K. (Amaranthaceae),  $\times 3,550$ .



equal in significance to the pigment dichotomy or the plastid similarity, but there is unmistakable evidence of a very close tie between the Caryophyllaceae and the Amaranthaceae.

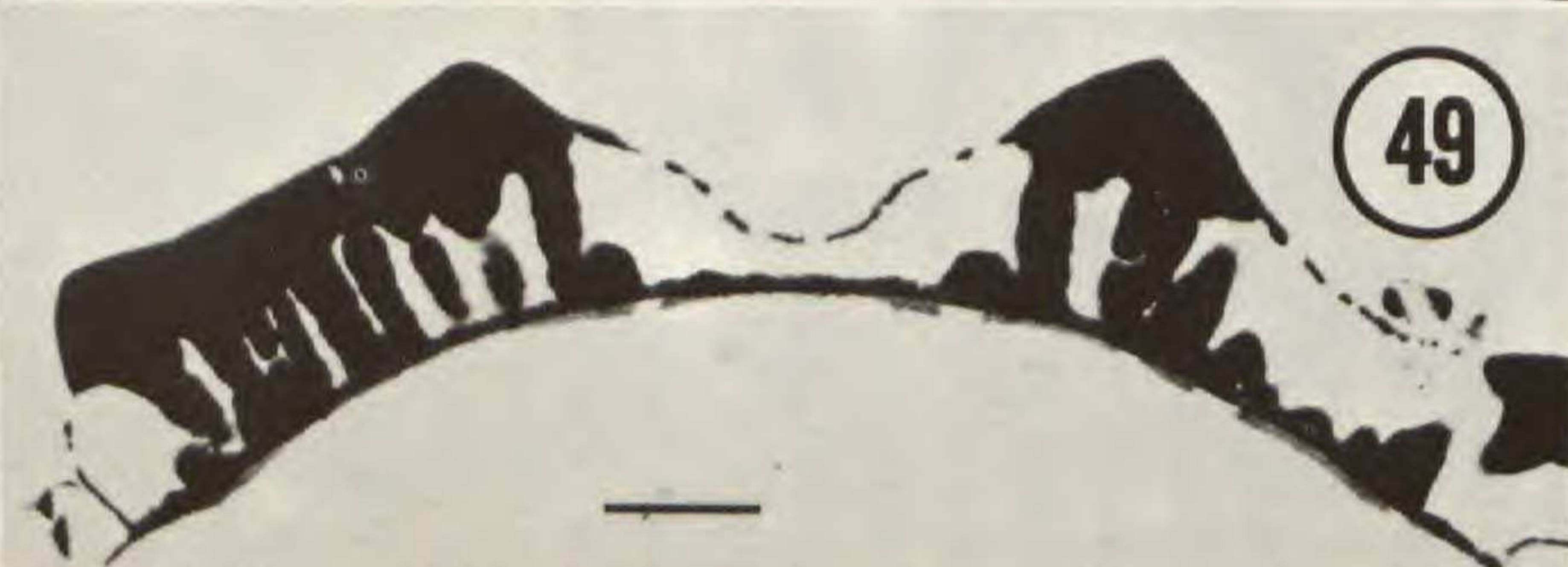
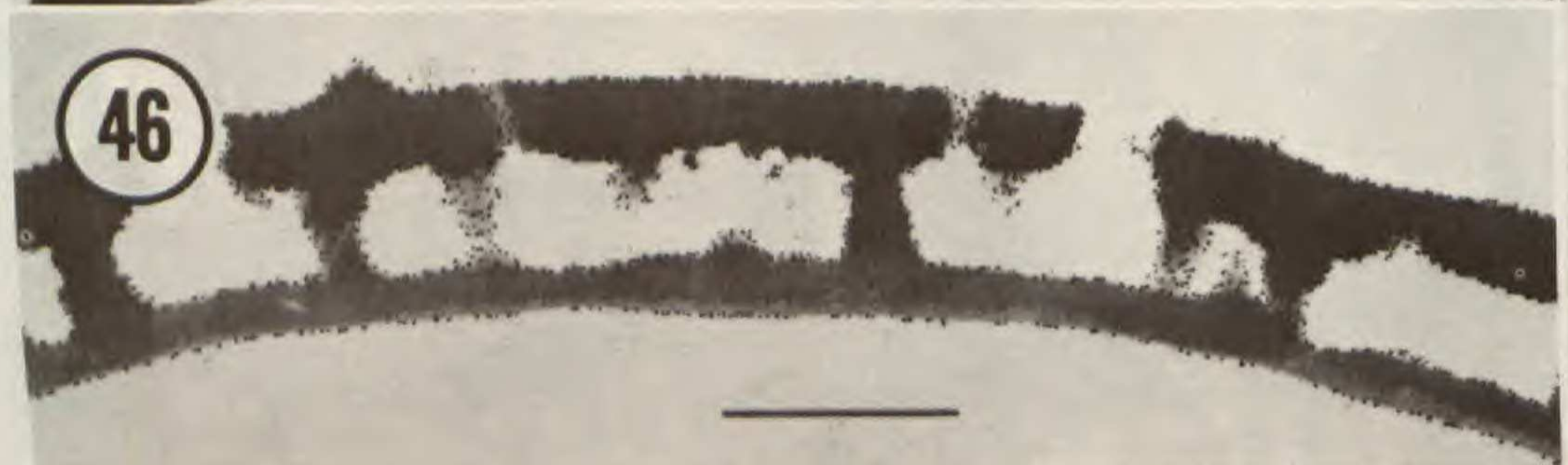
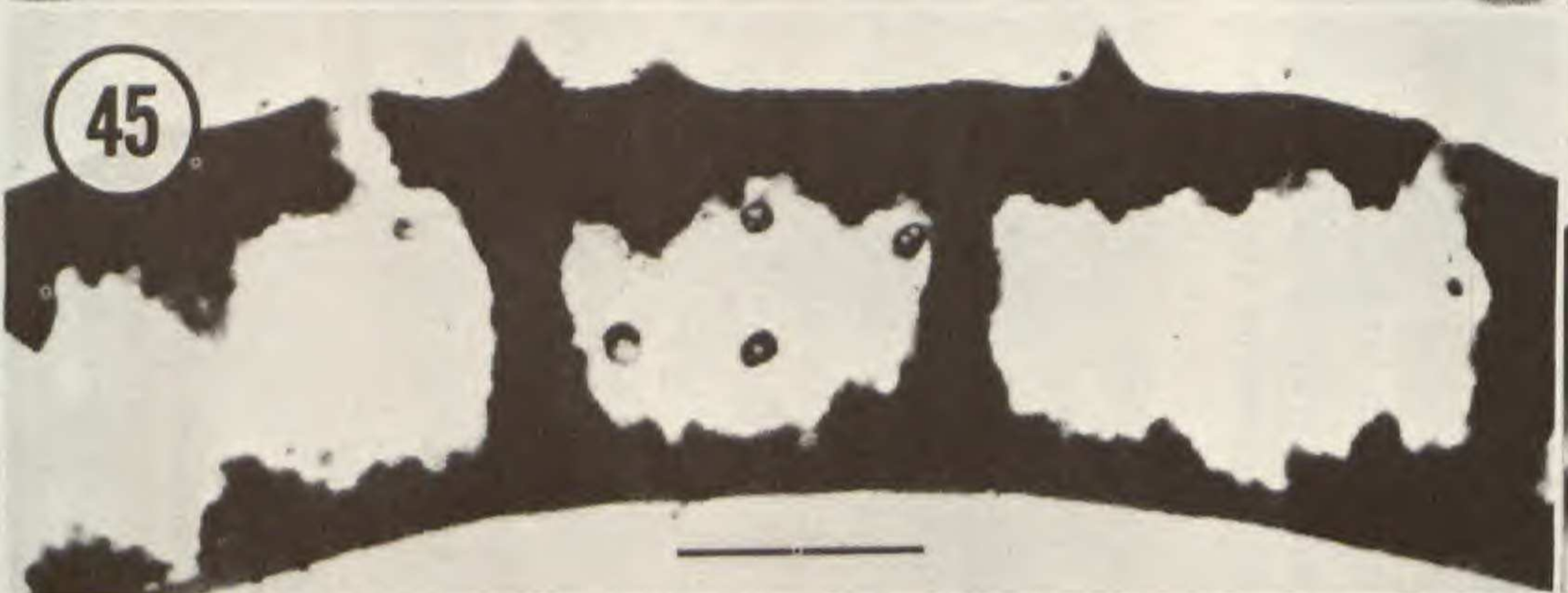
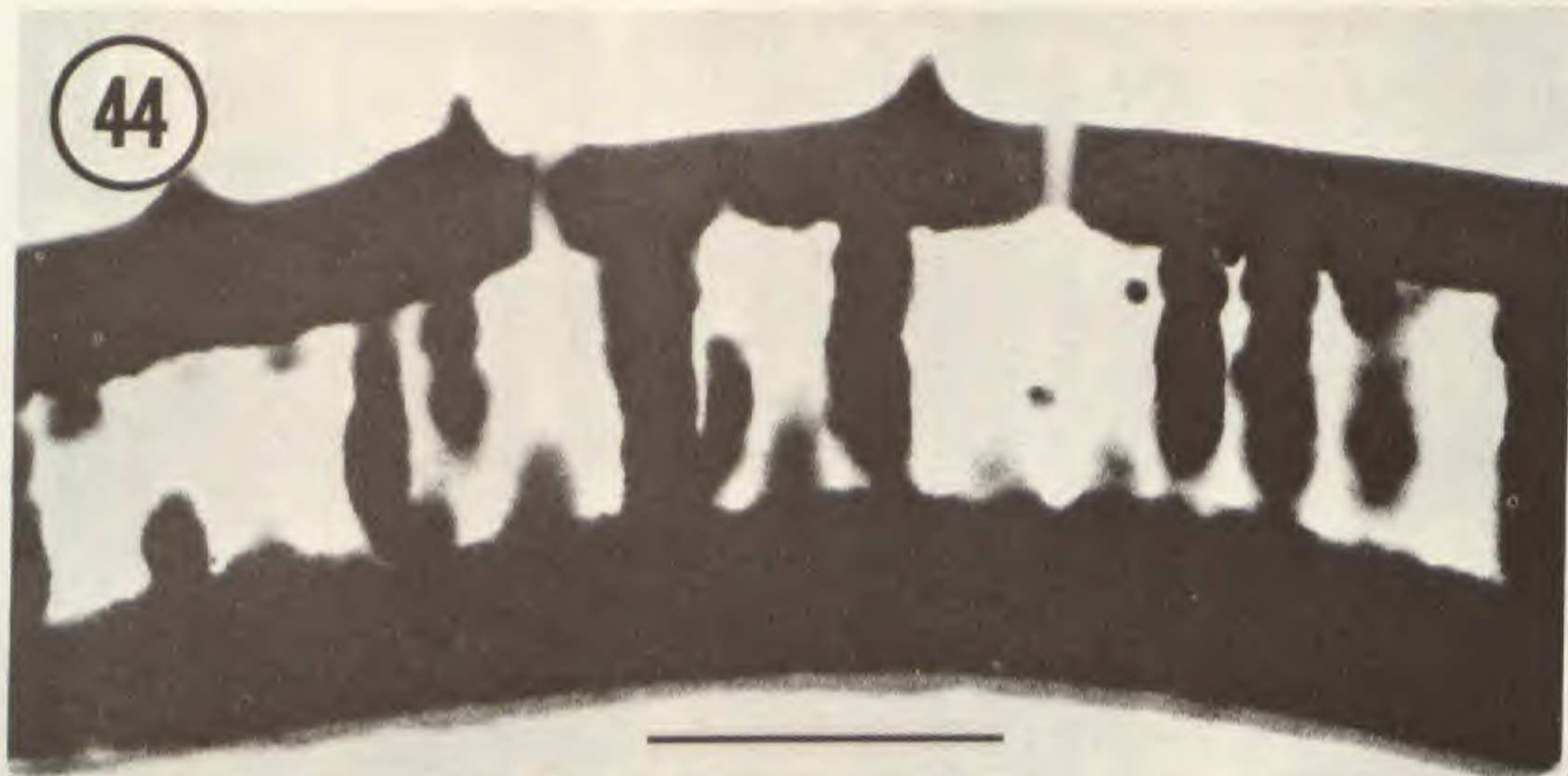
*Siphonochia* is a small caryophyllaceous genus of 5 or 6 species distributed along the warmer regions of the Atlantic seaboard. Six collections variously identified as *S. americana*, Fig. 27 (Nowicke & Skvarla, 1977: fig. 14), *S. diffusa* Fig. 26, *S. erecta*, *S. pauciflora*, Fig. 33, and *S. rugelii*, Fig. 32, were examined in LM and SEM; *S. americana* was also examined in TEM, Figs. 50 and 51. Two distinctive, yet related pollen types were found. The first type consists of grains with small (relative to the other type) pores, ca. 20 to 24(?) in number, deeply (relative to the other type) sunken, each pore separated from the adjacent ones by a single(?) row of columellae with a "tectum" that extends down their sides. Examples of this type include: *S. diffusa*, Fig. 26, *S. erecta*, and *S. rugelii*, Fig. 32. The close similarity of these specialized grains to those found in the amarantaceous taxa, *Gomphrena elegans*, Fig. 29, and *Pfaffia iresinoides*, Fig. 35, is remarkable. The second pollen type, found in *S. americana*, Fig. 27, and *S. pauciflora*, Fig. 33, is characterized by larger pores, fewer in number, with each delimited by a ringlike border having a fringe of small spines. *Alternanthera flavescens*, Fig. 36, from the Amaranthaceae, is almost indistinguishable from *S. americana* and *S. pauciflora*. Other closely related taxa include *Iresine angustifolia*, Fig. 30, *Tidestromia lanuginosa* (Nowicke, 1975: fig. 52), and *T. oblongifolia* (unpublished data). The thin sections of *S. americana*, Figs. 50 and 51, reveal a reduction of mesoporous exine similar to that in *Gomphrena elegans*, Fig. 49, and in *Iresine angustifolia*, Figs. 52 and 53.

To regard this type of similarity, a highly specialized pollen morphology not found elsewhere in the Centrospermae, in any of the other families examined in these studies, or in the literature (to the best of our knowledge), as parallelism is absurd.

Few taxonomists would dispute the close relationship of the Amaranthaceae and Chenopodiaceae, frequently cited as an example of "twin families." Yet the results from this palynological investigation suggest that the Amaranthaceae and Chenopodiaceae are more closely related to certain separate groups in the Caryophyllaceae than they are to each other. Surely the *Siphonochia-Alternanthera, Gomphrena, Pfaffia, Iresine* bond is more substantial than that of *Amaranthus-Chenopodium*. And, while the pollen morphology found in *Anabasis setifera*, Fig. 28, *Halocharis* spp. (unpublished data), *Nitrophila occidentalis*, Fig. 34, and *Traganum* (Nowicke, 1975: fig. 46) is less specialized than either the *Gomphrena* or *Siphonochia* types, the closest counterparts are found in the caryophyllaceous genera, *Cerastium* (Nowicke, 1975: fig. 32), *Drypis* (Nowicke, 1975: fig. 34), *Gymnocarpos* (Nowicke & Skvarla, 1977: fig. 4), *Paronychia fastigiata*, Fig. 31,

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FIGURES 37-43. Transmission Electron Micrographs of Centrospermae pollen.—37. *Gisekia pharnaceoides* L. (Aizoaceae),  $\times 6,480$ .—38. *Tetragonia vestita* I. M. Johnston (Aizoaceae),  $\times 3,600$ .—39. *Ceraria fruticulosa* Pears. & Steph. (Portulacaceae),  $\times 13,680$ .—40. *Boerhaavia erecta* L. (Nyctaginaceae),  $\times 4,340$ .—41. *Beta vulgaris* L. (Chenopodiaceae),  $\times 10,080$ .—42. *B. vulgaris*,  $\times 10,080$ .—43. *Alluaudia humbertii* Choux (Didiereaceae),  $\times 3,800$ .





*Sclerocephalus arabicus*, Fig. 25, and *Scleranthus perennis* (Nowicke, 1975: fig. 31), not in the Amaranthaceae.

However, data from all (?) other sources—pigment, plastid subtype, floral morphology—favor the Amaranthaceae-Chenopodiaceae relationship.

#### CACTACEAE

The Cactaceae was the last major family in which betalains were discovered and its subsequent transfer to the Centrospermae was agreeable to generalists and specialists alike.

This large family, native to the New World, is widely distributed in the arid regions, but is cultivated extensively as ornamentals in the Old World. Generic concepts vary considerably in the Cactaceae, from 50 to as many as 220, and the recognized number of species varies from at least 1,200 to perhaps as high as 2,000. Britton & Rose (1920) described the Cactaceae in a semimonographic treatment in which they recognized approximately 100 genera segregated in three tribes: Pereskieae with only the genus *Pereskia*; Opuntieae with seven genera; and the Cereeae with the remaining and vast majority of genera.

Nowicke (1975) examined the pollen of 12 species. The range of variation illustrated (Nowicke, 1975: figs. 19–24) is, for the most part, representative of the family: the common type of tectum (figs. 19–22), spinulose and punctate/perforate, is distributed across the three aperture types, pantoporate (figs. 19–20), 3-colpate (fig. 21), and pantocolpate (fig. 22). A specialized type in the Cactaceae, polygonal in shape due to the very large, flat apertures which are separated from each other by an incomplete tectum of a reticulate configuration, is illustrated by *Opuntia polycantha* and *O. engelmanni* (Nowicke, 1975: figs. 23–24) in this paper by *Opuntia lindheimeri*, Figs. 21, 57.

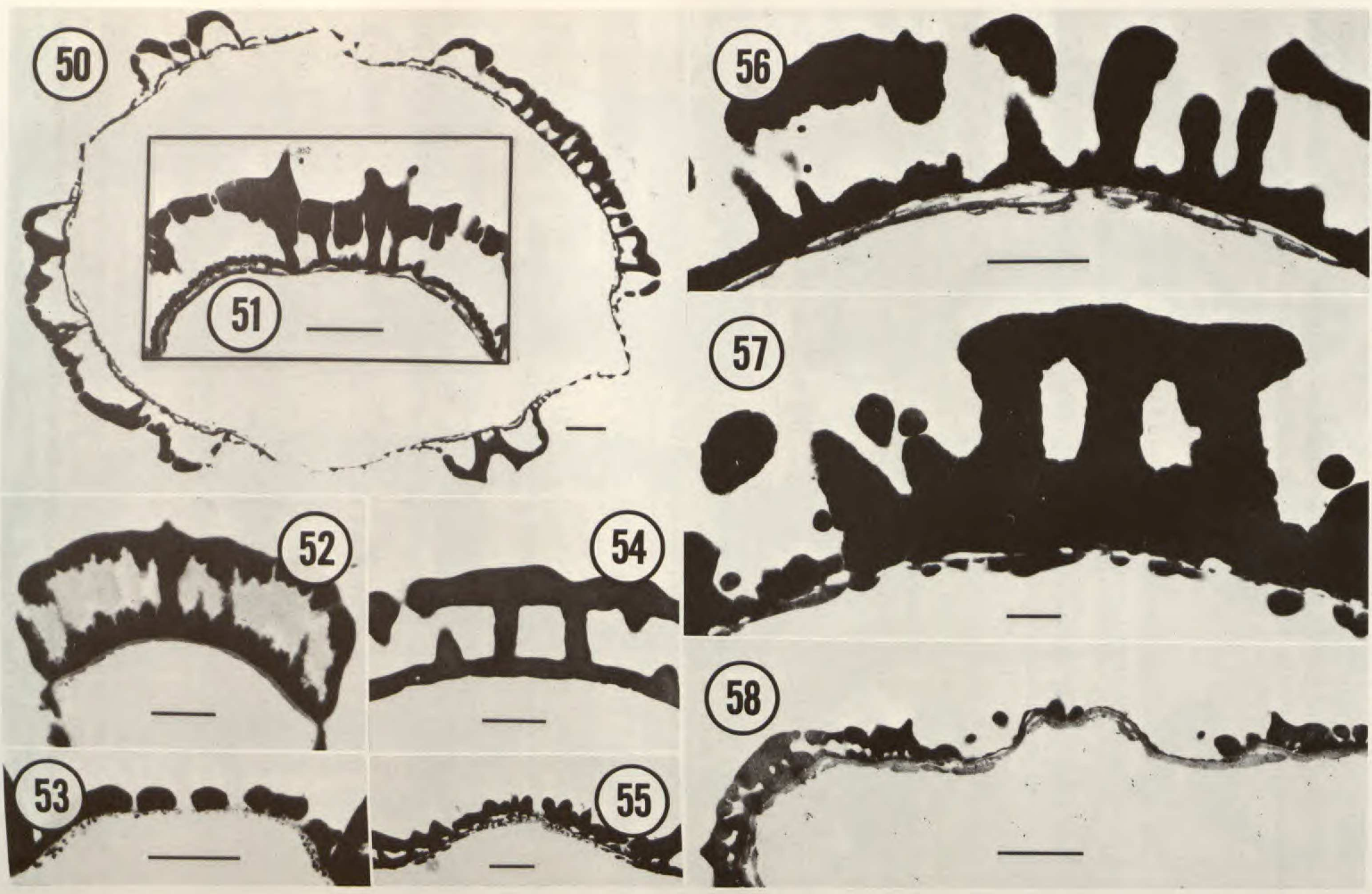
In thin section (Skvarla & Nowicke, 1976) *Opuntia fulgida* (fig. 20) and *Echinocereus cinerascens* (fig. 21) have an exine structure consistent with the spinulose, perforate exomorphology.

The structure of the aperture in the Cactaceae is very similar (Skvarla & Nowicke, 1976: fig. 20; Nowicke & Skvarla, 1977: fig. 22) to that in the Didiereaceae, Fig. 43, *Alluaudia humbertii* (see also Skvarla & Nowicke, 1976: fig. 28).

Leuenberger (1976) investigated the pollen of more than 600 species of Cactaceae and produced a classic and definitive study. Many of the important collections of Britton and Rose are deposited at the US National Herbarium and, to the extent possible, Nowicke accommodated Leuenberger's request for pollen samples from critical taxa. However, the holdings at US do not have sufficient depth to permit duplication of efforts and our investigation was terminated. The phrase "readily obtainable" in reference to source material (see Introduction) is

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FIGURES 44–49. Transmission Electron Micrographs of Centrospermae pollen.—44. *Salpianthus arenarius* H. & B. (Nyctaginaceae),  $\times 23,220$ .—45. *Cometes surattensis* L. (Caryophyllaceae),  $\times 16,340$ .—46. *Phytolacca americana* L. (Phytolaccaceae),  $\times 15,200$ .—47. *Stegnosperma halimifolium* Benth. (Phytolaccaceae),  $\times 3,000$ .—48. *Anabasis setifera* Moq. (Chenopodiaceae),  $\times 20,520$ .—49. *Gomphrena elegans* Mart. (Amaranthaceae),  $\times 8,460$ .



not to be interpreted as infinite. His report of tetrads in *Pseudorhipsalis himantoclada* (Leuenberger, 1976: 293, plate 13) is not only the first in the family but in the order Centrospermae. Comparison of Leuenberger's (1976, plates 15–18) SEMs of the Cactaceae tectum at high magnification with that of other families in the Centrospermae (Nowicke, 1975: figs. 73–81; Nowicke & Skvarla, 1977: figs. 7–12) should remove any vestige of doubt as to the very close relationship between this family and those remaining in the Centrospermae.

#### AIZOACEAE AND MOLLUGINACEAE

The definition, the boundaries, and the constituent genera of two families, Aizoaceae and Molluginaceae, vary according to the author, and seemingly no two are in complete agreement. At the one extreme, Pax & Hoffman (1934) relegated the latter to subfamily status under the former, and at the other extreme, some of the larger genera, *Tetragonia*, *Mesembryanthemum*, etc., are elevated to family status by various authors. The Molluginaceae has been characterized as an anthocyanin family and the Aizoaceae as a betalain family, but the assignment of genera on the basis of the pigment dichotomy applies only to those genera whose pigments have been identified.

Due primarily to lack of material, the pollen morphology in both families was discussed only briefly in the previous publications (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977). The pollen of an additional 15 species representing 9 genera has been examined, Table 1. All taxa from this alliance have the spinulose and punctate/perforate tectum, and with the single exception of *Mollugo verticellata*, which is pantocolpate (Nowicke, 1975: fig. 41), all are 3-colpate.

Species illustrated include: *Gisekia pharnaceoides*, Figs. 1–2, 37; *Tetragonia vestita*, Figs. 3–4, 38; and *Delosperma ecklonis*, Fig. 23. In TEM *Tetragonia*, Fig. 38, has a very thin foot layer in contrast to that found in *Gisekia*, Fig. 37, or in *Mesembryanthemum* (Nowicke & Skvarla, 1977: fig. 19). In Figs. 37 and 38 the endexine is most conspicuous in the aperture regions, but *Mesembryanthemum* (Nowicke & Skvarla, 1977: fig. 19) has a readily defined endexine in what appears to be the mesocolpus.

The pollen of one species of *Acrodon*, *A. bellidiflorus* (Nowicke & Skvarla, in press), and three of *Delosperma*, *D. abyssinica*, *D. ecklonis*, Fig. 23, and *D. mahonii*, was obtained from the herbarium at Kew. Species from these two genera were described as having a reticulate exine by Radulescu (1973). The grain illustrated in Fig. 23 is representative of *Delosperma*; the sample of *Acrodon* contained some grains with slightly larger perforations. Whether the Aizoaceae has pollen with reticulate exines depends on the definition of reticulate. But we would describe the tectum in all four as spinulose and perforate.

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FIGURES 50–58. Transmission Electron Micrographs of Centrospermae pollen.—50. *Siphonochia americana* (Nutt.) T. & G. (Caryophyllaceae),  $\times 5,740$ .—51. *S. americana*,  $\times 10,260$ .—52. *Iresine angustifolia* Euphr. (Amaranthaceae),  $\times 8,740$ .—53. *I. angustifolia*,  $\times 12,600$ .—54. *Basella excavata* S. Ell. (Basellaceae),  $\times 8,120$ .—55. *B. excavata*,  $\times 6,670$ .—56. *Reichenbachia hirsuta* Spreng. (Nyctaginaceae),  $\times 13,630$ .—57. *Opuntia lindheimeri* Engelm. (Cactaceae),  $\times 7,560$ .—58. *Herniaria glabra* L. (Caryophyllaceae),  $\times 19,760$ .



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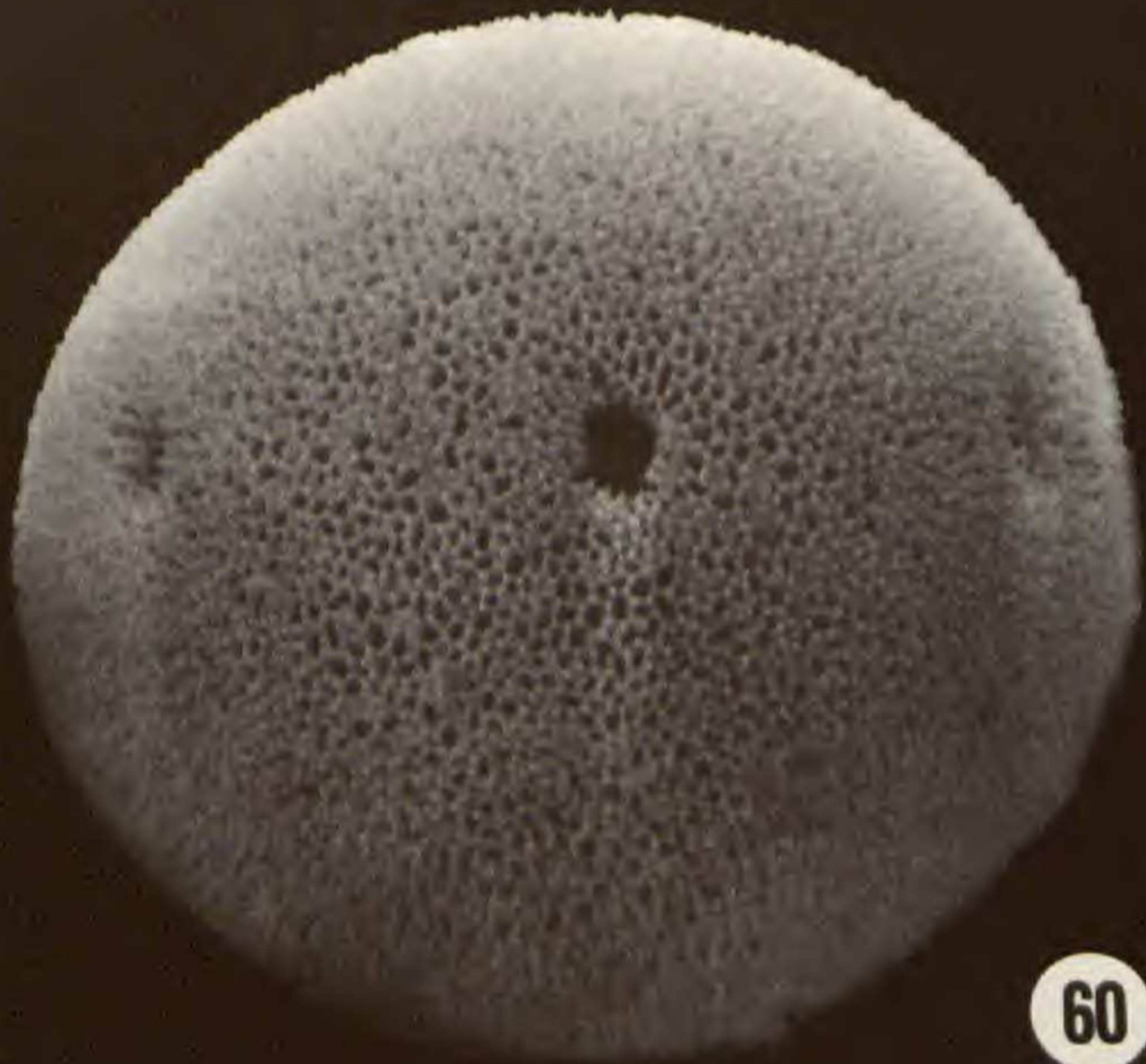
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## BASELLACEAE

One of the more unusual pollen morphologies in the dicots is found in the small tropical family Basellaceae. Collections identified as *Basella alba* and *B. rubra* have a well-defined cuboidal shape with a colpus on each of the six faces (Nowicke, 1975: figs. 63–65). *Basella excavata*, Fig. 22, has a similar morphology, but the tectum is almost complete (indented punctae), and in thin section, Fig. 54, this species has a readily identified foot layer, columellae, and tectum. A granular endexine is present only in the region of the aperture, Fig. 55. All other members of this family, *Anredera cordifolia* (Nowicke, 1975: fig. 61), *Ullucus tuberosus* (Nowicke, 1975: fig. 62), and *Anredera scandens* (Nowicke & Skvarla, 1977: fig. 3) have the characteristic spinulose/punctate tectum of the order.

## DIDIEREACEAE

The pollen of the Didiereaceae can be distinguished from all other Centrospermae by the apertures, 5–7 zonocolpate. This small family, four genera and ten species endemic to Madagascar, is characterized by a succulent habit, and successful grafting experiments with the Cactaceae supports the contention that these two families are closely related, regardless of the geographical distribution.

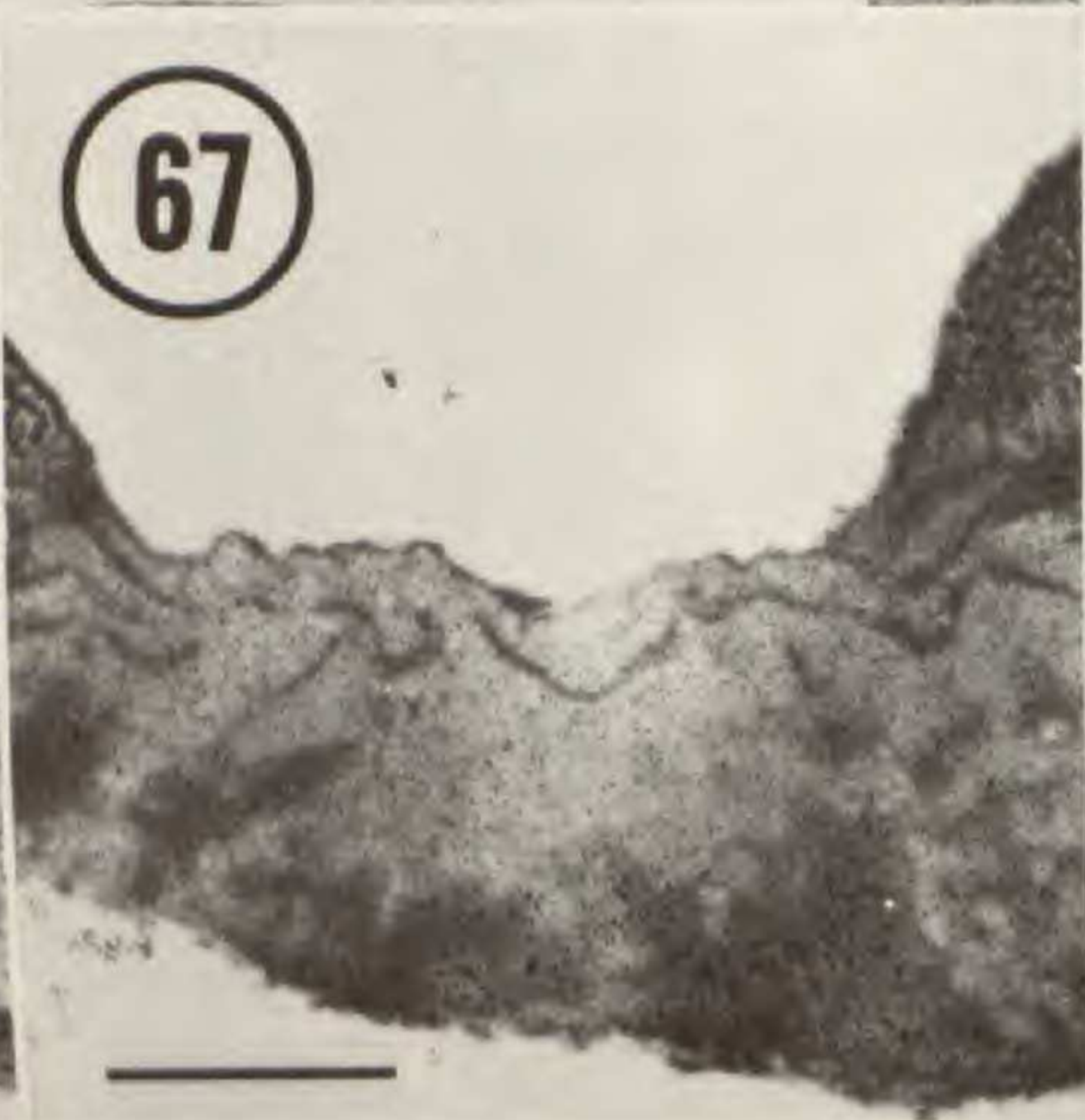
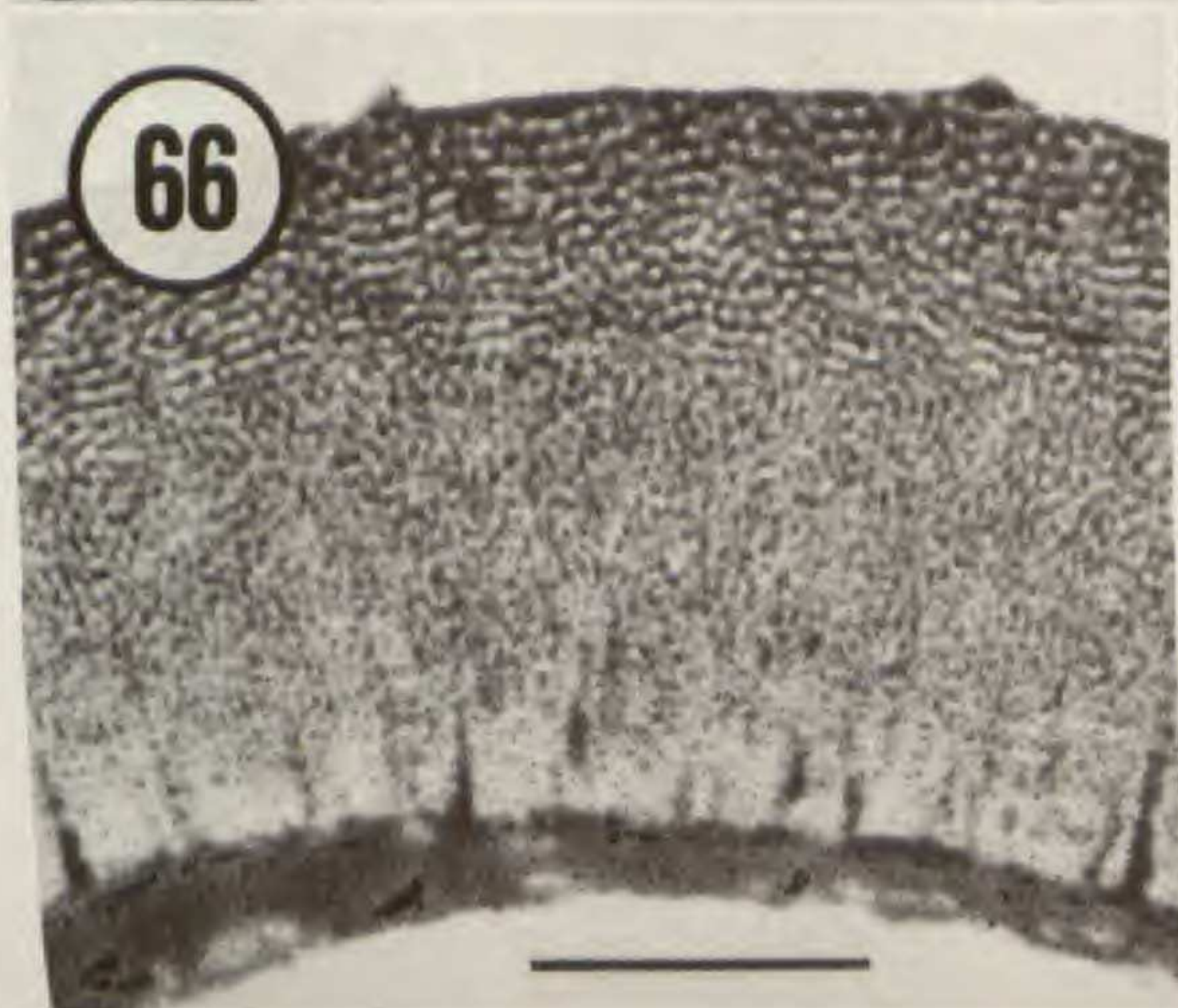
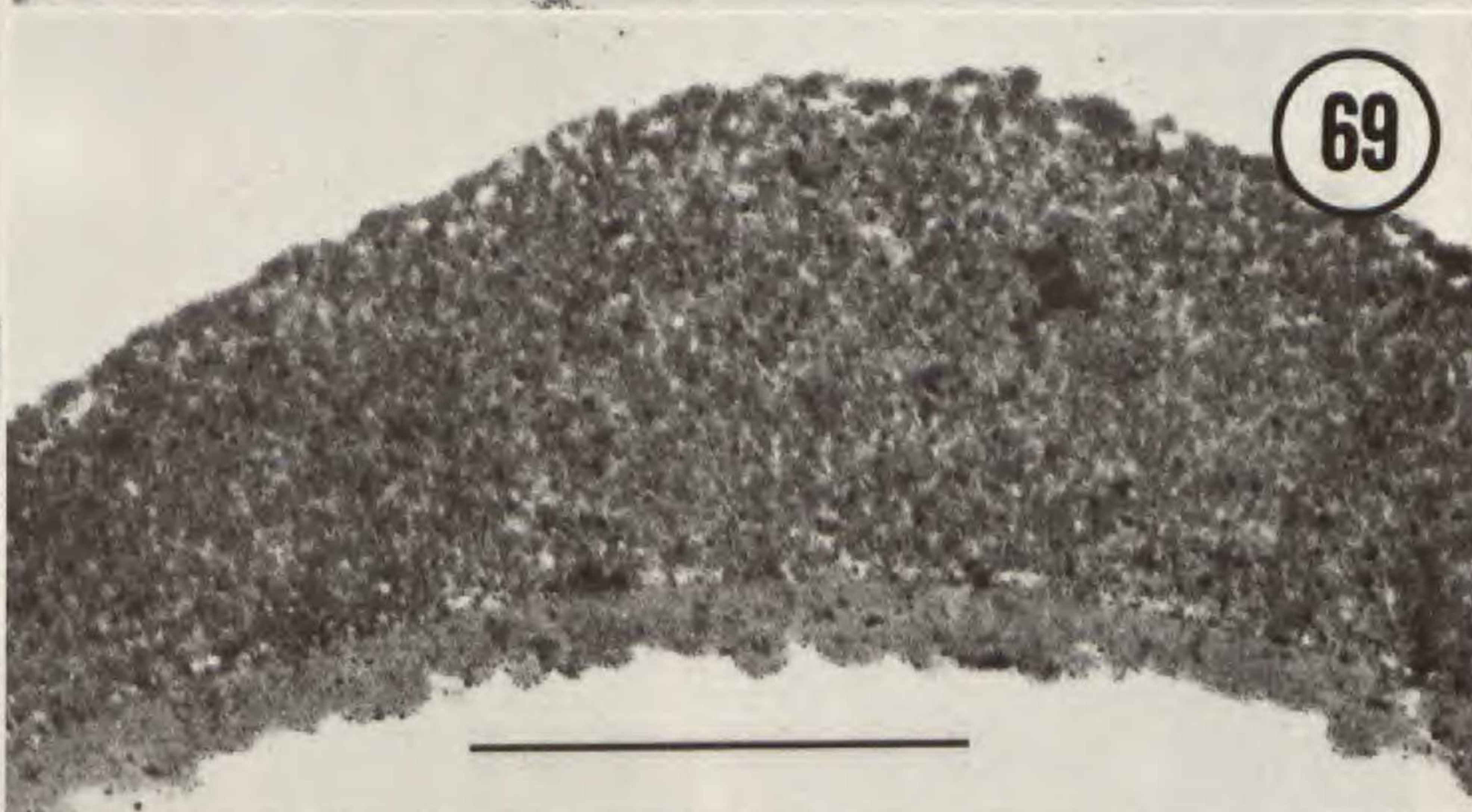
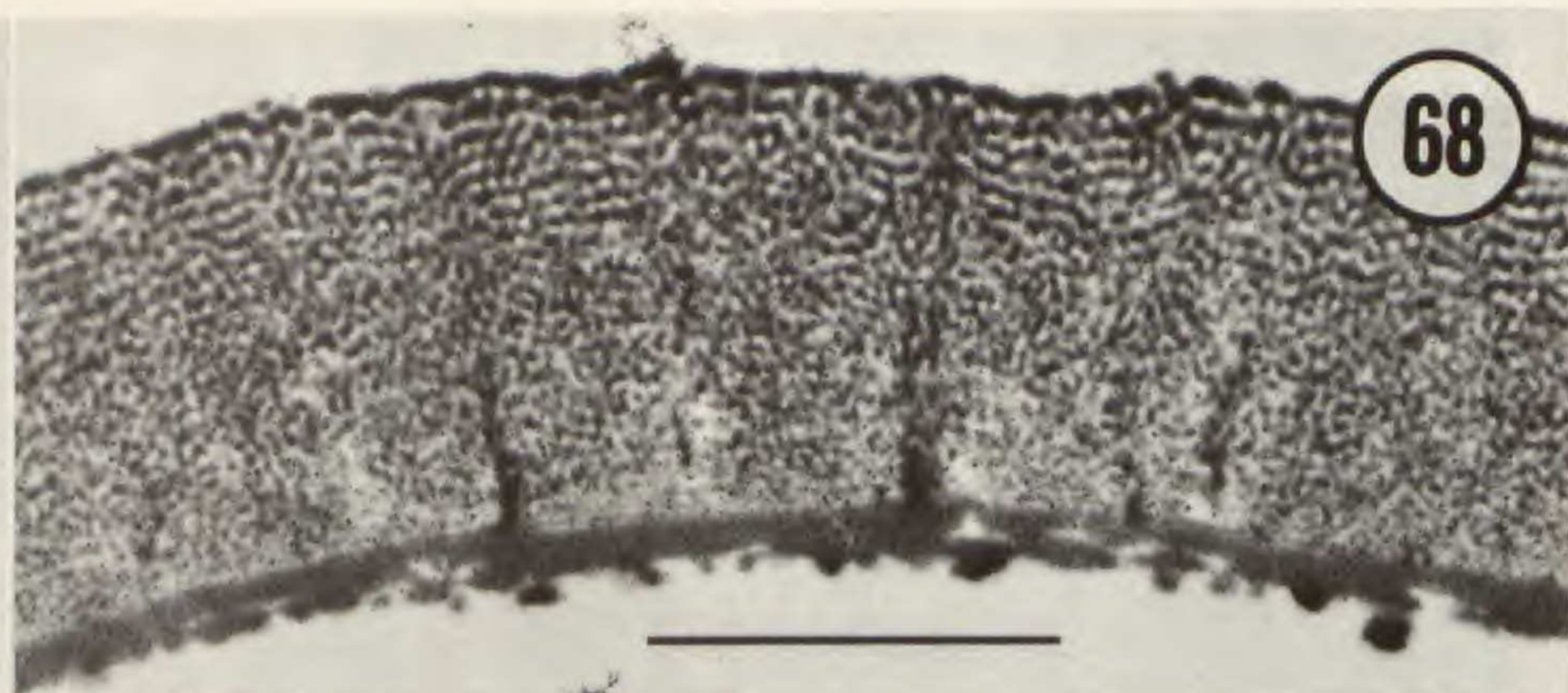
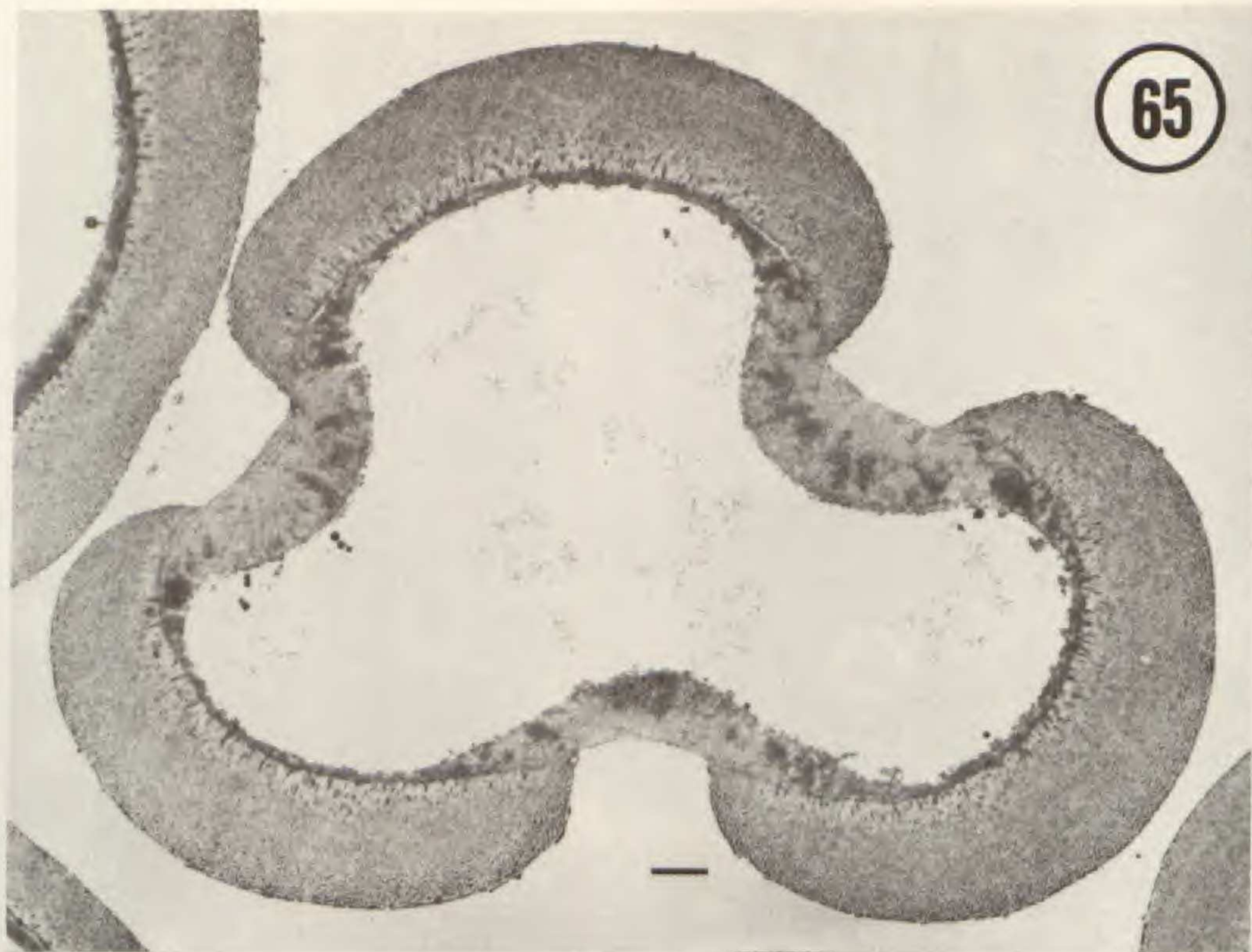
Based on the examination of three species representing two genera, *Alluaudia humbertii*, Figs. 11–12, 43, *A. procera* (Nowicke, 1975: figs. 66, 80; Skvarla & Nowicke, 1976: fig. 28), and *Decarya madagascariensis* (unpublished data) the pollen morphology, a spinulose and perforate tectum, confirms its inclusion in the Centrospermae by all recent generalists.

## HALOPHYTACEAE

The Halophytaceae, a monotypic family in temperate South America, has a pollen morphology distinguished by a cubelike shape with a large pore on each of the six faces (Skvarla & Nowicke, 1976: fig. 3). In TEM (Skvarla & Nowicke, 1976: fig. 29) the structure of the exine is similar to some members of the Chenopodiaceae: a thick tectum supported by stout columellae on a thin foot layer underlain by a fragmented lamellar endexine. However, the sieve-tube plastid in the Halophytaceae has a globular central crystalloid in contrast to the Amaranthaceae and Chenopodiaceae, which lack this particular inclusion (Behnke, 1976). Since no other taxa examined thus far in the Centrospermae have pollen with this shape and aperture arrangement, we would agree with separate family status (Takhtajan, 1969).

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FIGURES 59–64. Scanning Electron Micrographs of Achatocarpaceae, Batidaceae, Gyrostemonaceae, and Theligonaceae pollen.—59. *Achatocarpus spinulosus* Grisebach (Achatocarpaceae),  $\times 2,400$ .—60. *Theligonum cynocrambe* L. (Theligonaceae), equatorial view,  $\times 2,310$ .—61. *Batis maritima* L. (Batidaceae), equatorial view,  $\times 2,770$ .—62. *Gyrostemon australasicus* (Moq.) Heimerl (Gyrostemonaceae), polar view,  $\times 2,310$ .—63. *Codonocarpus attenuatus* H. Walter (Gyrostemonaceae), equatorial view,  $\times 1,850$ .—64. *Didymotheca pleiococca* F. Muell. (Gyrostemonaceae), polar view,  $\times 2,160$ .



## ACHATOCARPACEAE

*Achatocarpus* Triana and *Phaulothamnus* A. Gray are betalain genera which have been included in the Phytolaccaceae (Walter, 1909) or given separate family status as Achatocarpaceae (Heimerl, 1934; Eckhardt, 1964). According to Behnke (1976: figs. 6–7), both genera have the protein type of sieve-tube plastid characteristic of the Centrospermales. The presence of a globular central crystalloid eliminates a close tie to either Amaranthaceae or Chenopodiaceae, which lack this structure, and also to the Caryophyllaceae, which has a polygonal-shaped crystalloid.

The pollen morphology of *Achatocarpus* and *Phaulothamnus* is very similar: spheroidal shape, apertures consisting mostly of 4 to 6 large pores, but can be irregular, and a tectum which is scabrate (Bortenschlager et al., 1972; Nowicke, 1975: fig. 70) or very coarsely granular (unpublished data). The pollen is distinct from all other Centrospermales, but considering the range of variation in other families such as Nyctaginaceae, e.g., *Bougainvillea* (Nowicke, 1975: fig. 11), *Boerhaavia erecta*, Figs. 7–8, *Reichenbachia hirsuta*, Fig. 20; or Caryophyllaceae, e.g., *Cometes surattensis*, Fig. 17, *Siphonychia diffusa*, Fig. 26, *S. americana*, Fig. 27, *S. rugelii*, Fig. 32, *S. pauciflora*, Fig. 33, *Lychnis* (Nowicke, 1975: fig. 36); or Cactaceae (Nowicke, 1975: figs. 19–24), it would be difficult to justify the exclusion of *Achatocarpus* and *Phaulothamnus* from the Phytolaccaceae on this characteristic alone.

Only *Achatocarpus spinulosus*, Fig. 59, is illustrated in this paper.

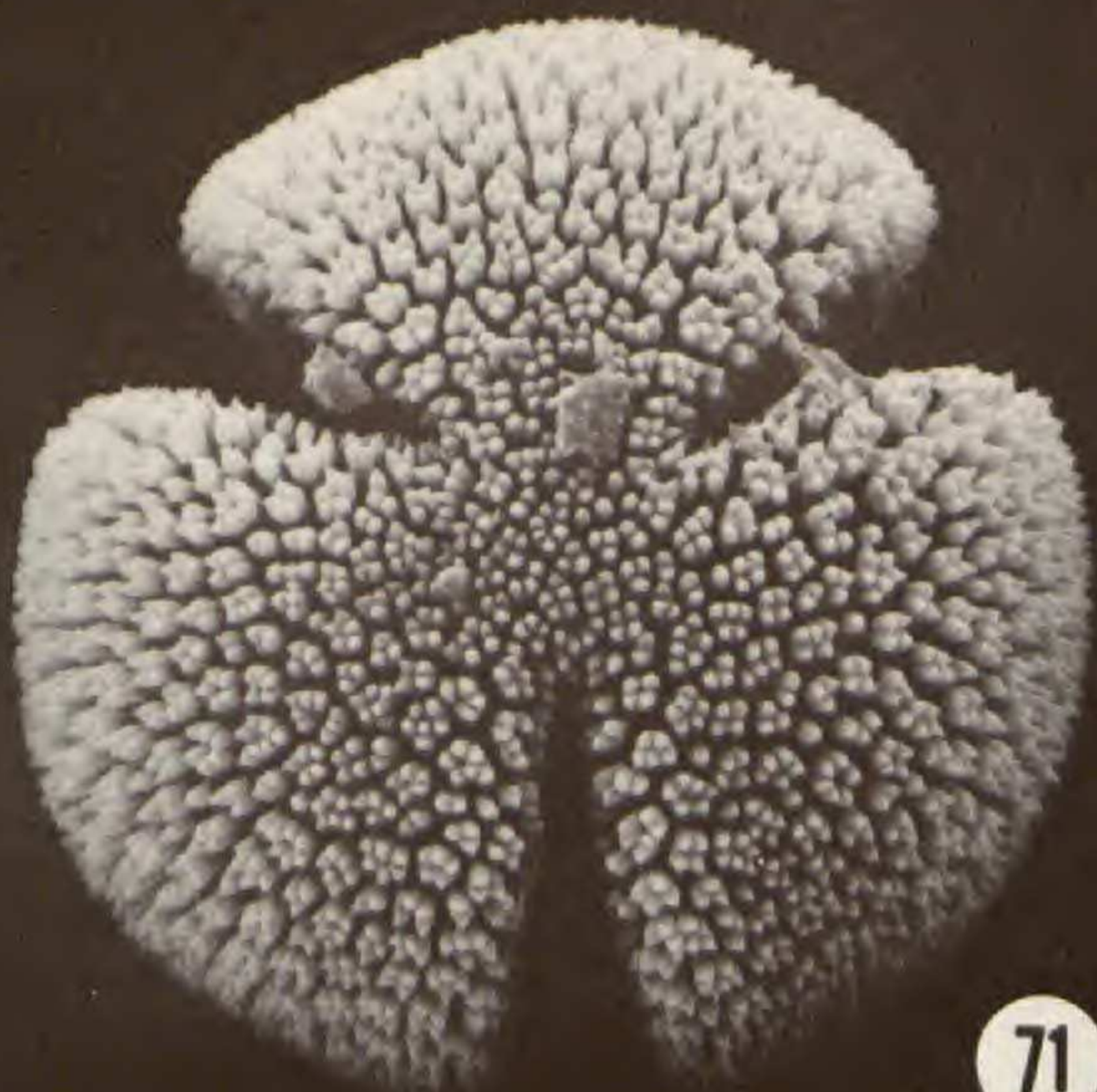
## THELIGONACEAE

Melchior (1964) included the Theligonaceae in the Myrtales near the Haloragaceae, and while Cronquist (1968) followed Melchior's suggestion, he also expressed some doubt as to the extent of the relationship between these two families.

The Theligonaceae have been the subject of several detailed investigations (Kapil & Mohana Rao, 1966; Praglowski, 1973; Wunderlich, 1971), but the classification remains controversial. The pollen morphology of *Theligonum cynocrambe*, Fig. 60, (3–)4–6(–7)-zonoporate with a tectum described as an illusory impression of a reticulum by Praglowski (1973), has no counterpart in all of the Centrospermales examined to date (see also Nowicke, 1975: figs. 71–72). This conclusion, together with the presence of anthocyanins and the starch type sieve-tube plastid, dismisses the possibility that the Theligonaceae are related to or derived from the Centrospermales. However, we have reservations about Wunderlich's (1971) proposal to treat *Theligonum* as a tribe in the Rubiaceae since neither the aperture condition nor the particular tectum as described above are known to occur in that family. In an unpublished study of 75 species in the tribe

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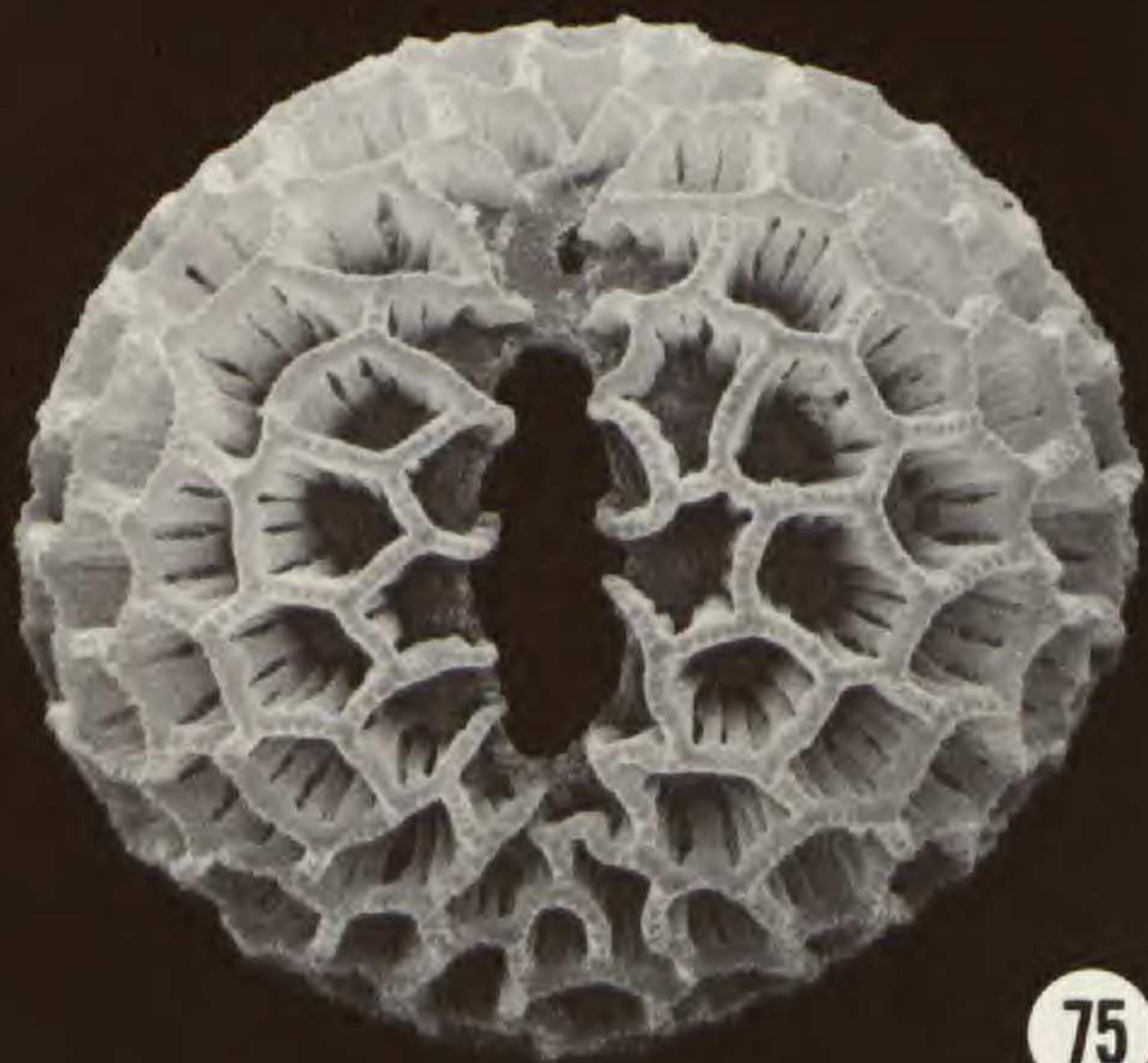
FIGURES 65–70. Transmission Electron Micrographs of Gyrostemonaceae and Batidaceae pollen.—65. *Didymotheca pleiococca* F. Muell. (Gyrostemonaceae),  $\times 4,300$ .—66. *D. pleiococca*,  $\times 15,580$ .—67. *D. pleiococca*,  $\times 11,400$ .—68. *Codonocarpus cotinifolius* (Desf.) F. Muell. (Gyrostemonaceae),  $\times 23,400$ .—69. *Batis maritima* L. (Batidaceae),  $\times 30,400$ .—70. *B. maritima*,  $\times 19,720$ .



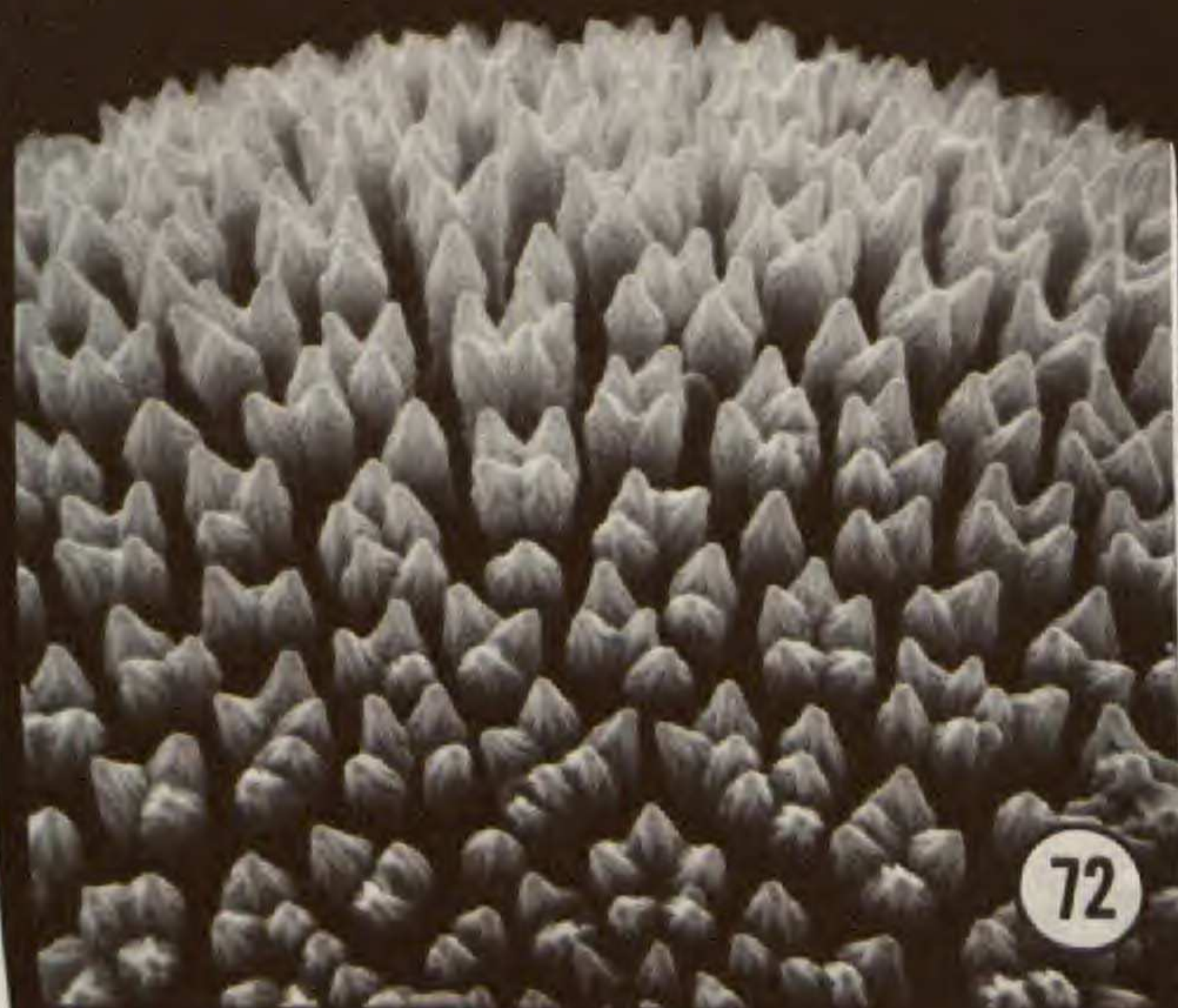
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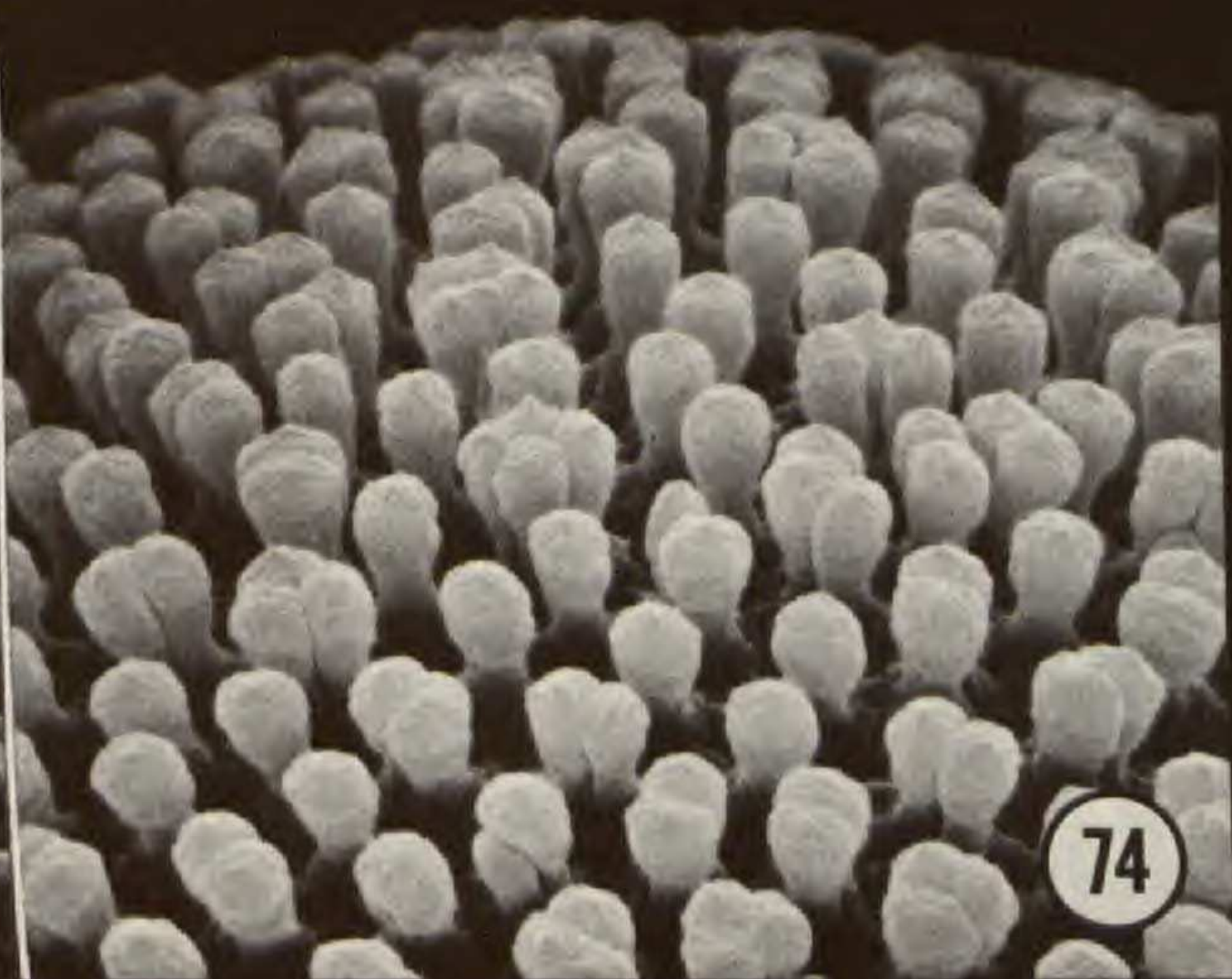
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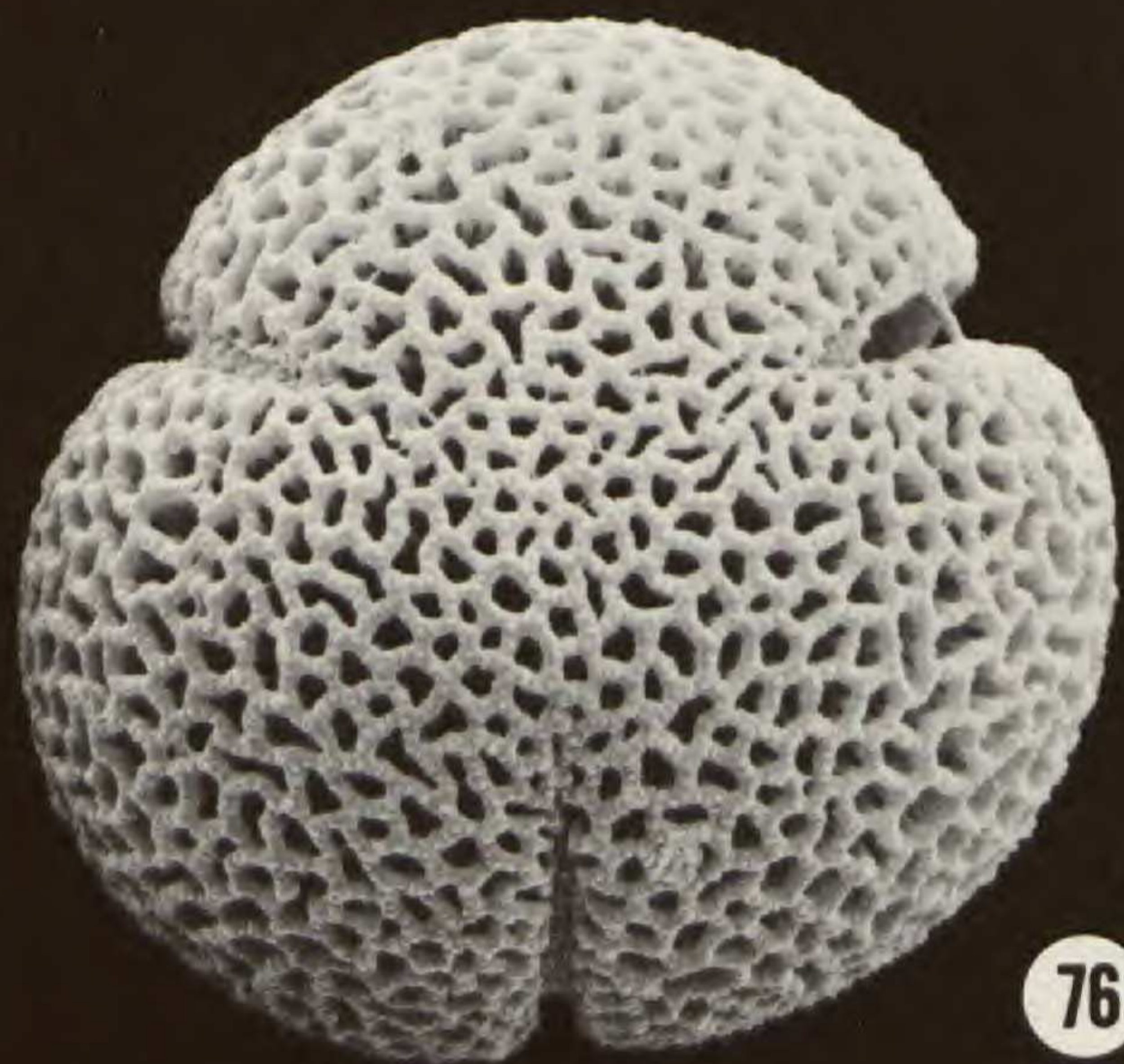
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Guettardeae and 16 in the Ixoreae, Nowicke found 3-porate grains in some species of *Guettardus*, but regards this condition as derived from 3-colporate due to a progression of intermediate forms. The 4–7-zonoporate aperture type found in *Theligonum* is another matter altogether. Furthermore, we are of the opinion that the tectum of the rubiaceous genera *Asperula*, *Athosperma*, and *Galium* (unpublished data) is not similar to that found in *Theligonum*.

Pragłowski (1970), who described the pollen morphology of the Haloragaceae as well as Theligonaceae, did not consider the two families to be closely related. However, we are of the opinion that the Theligonaceae is more likely to be related to the Haloragaceae than to the Rubiaceae. At least the Haloragaceae has taxa with this aperture type (Pragłowski, 1970: plate 7, fig. 2) and possibly even the tectum (Pragłowski, 1970: plate 13, figs. e, f).

The only point on which all investigators seem to agree is the distinction of this small family of two or three species.

#### BATIDACEAE AND GYROSTEMONACEAE

The general agreement that neither the Batidaceae nor Gyrostemonaceae belong in the order Centrospermae is not surprising since both lack the betalains, both have the starch type sieve tube plastid, and each has a chromosome number other than the  $x = 9$  for the centrospermous families: Batidaceae  $x = 11$ , and Gyrostemonaceae  $x = 14$ . The present controversy concerns the extent of their relationship to each other, if any, and their placement in the dicot hierarchy.

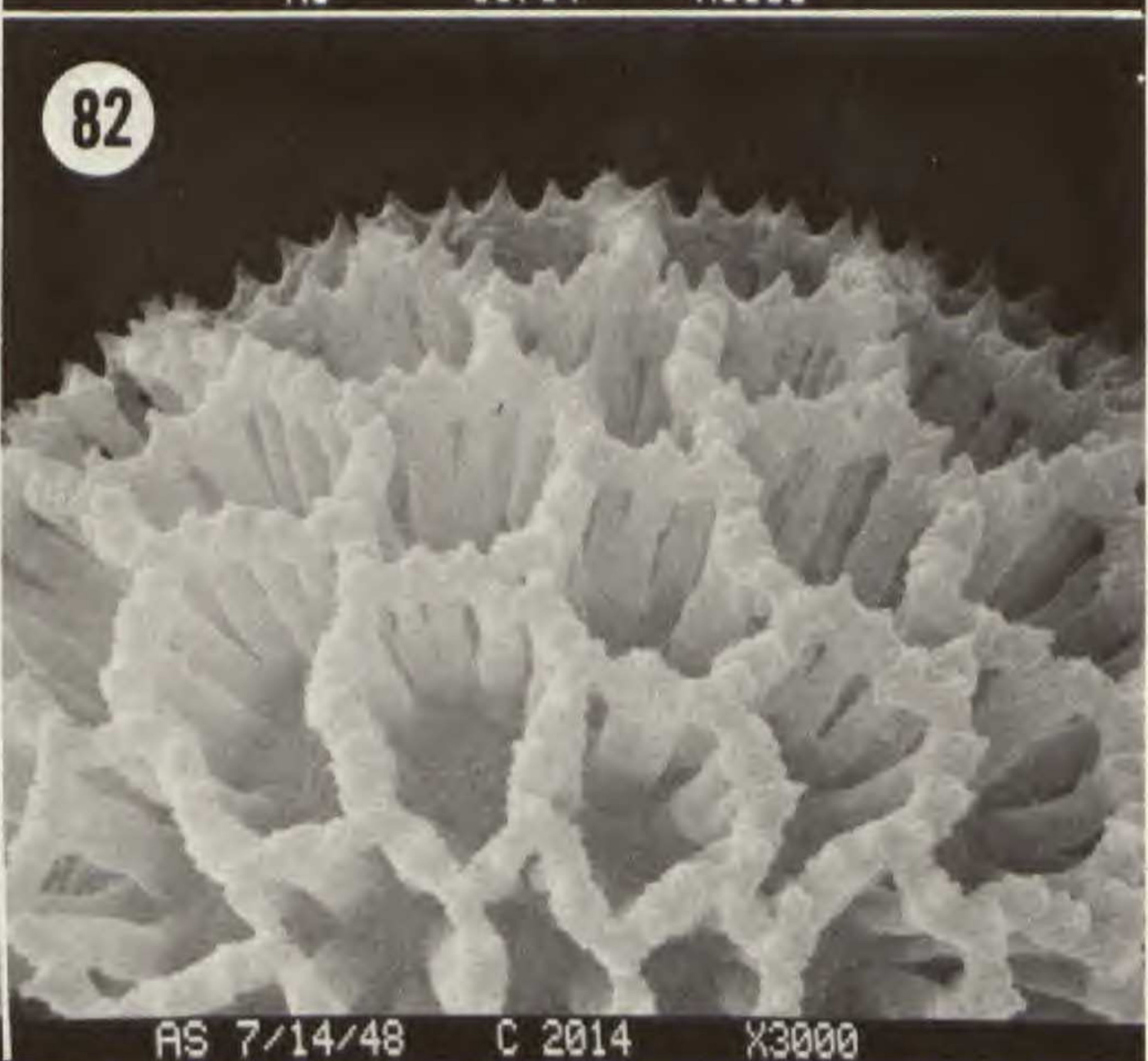
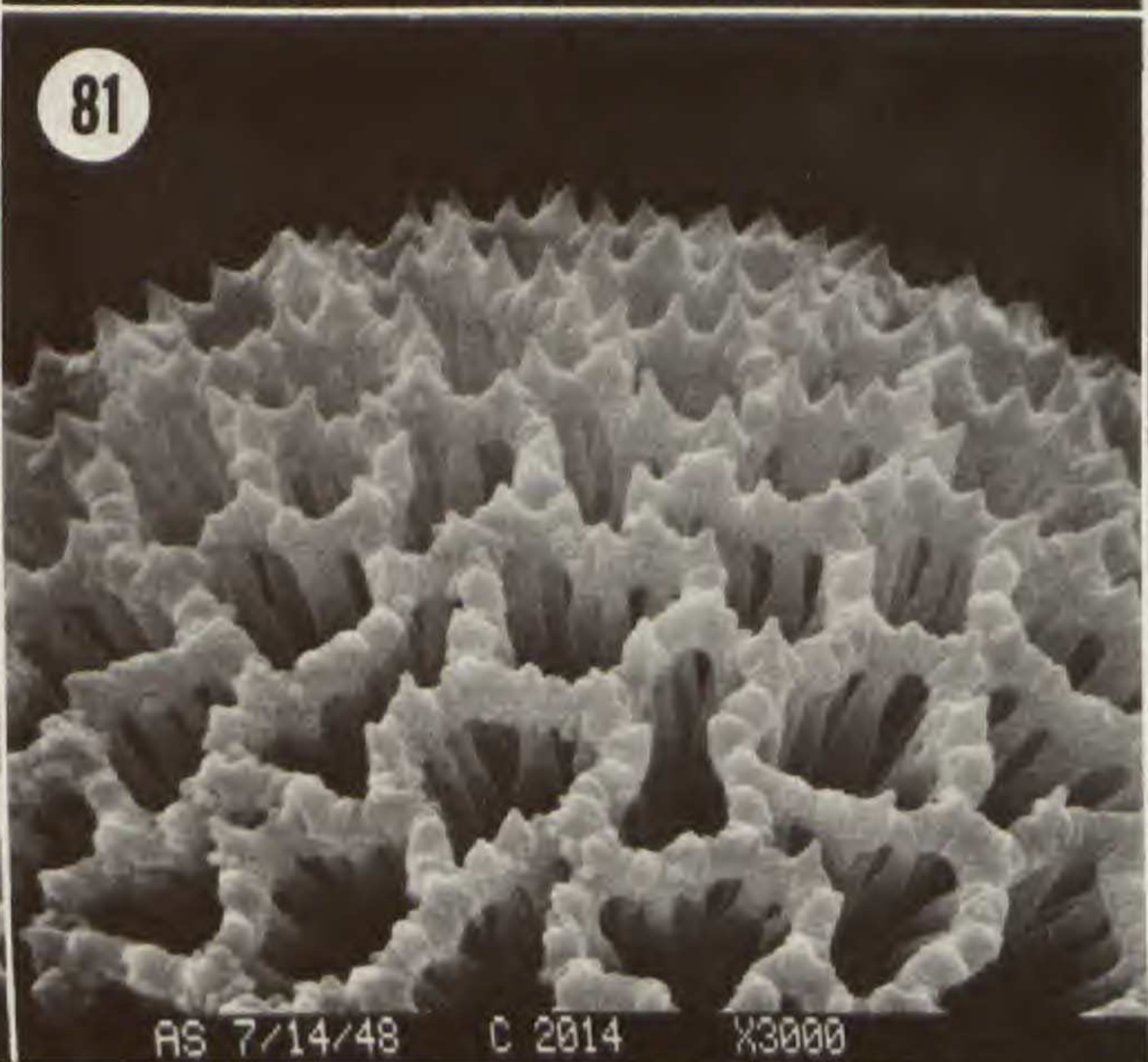
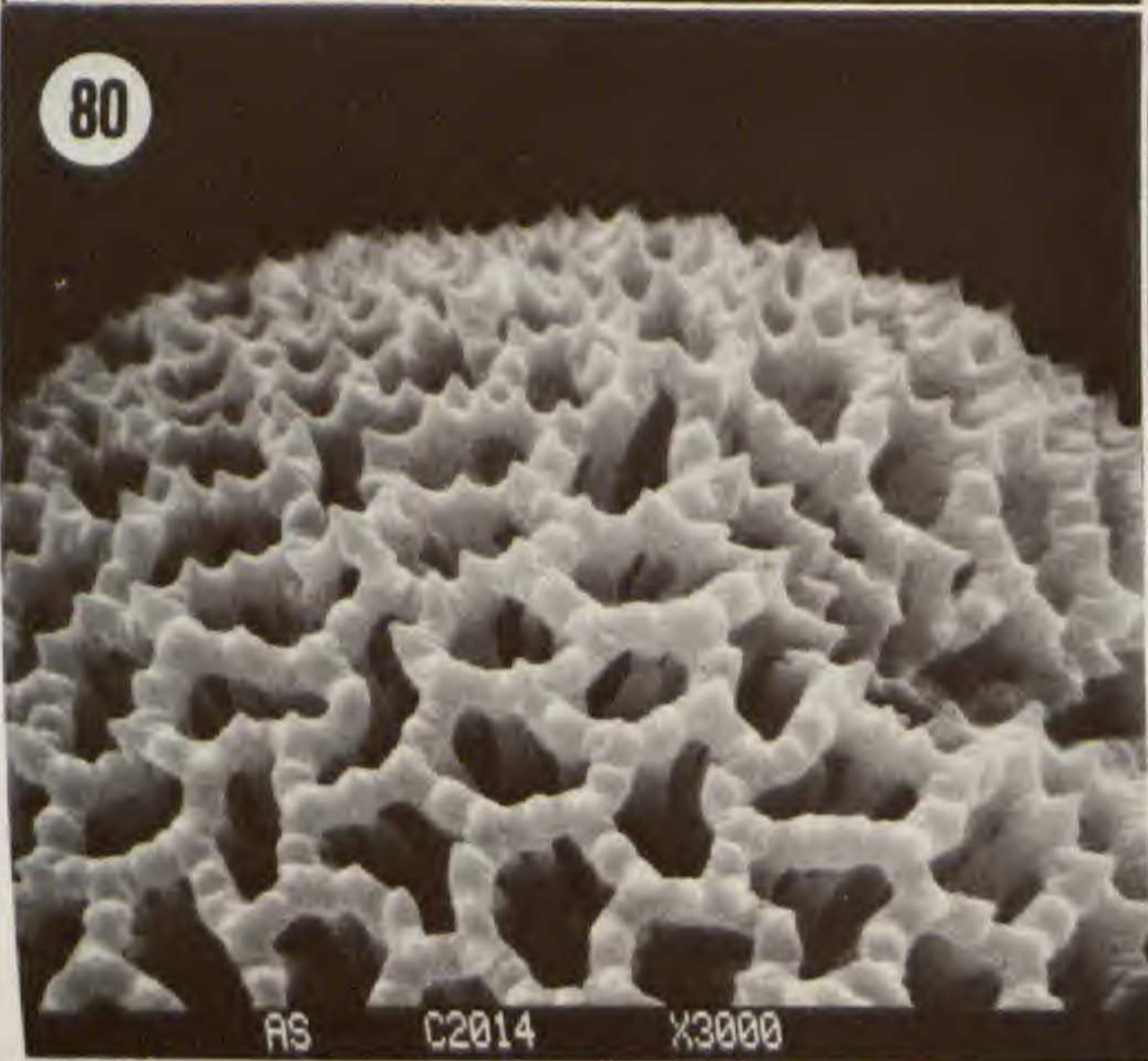
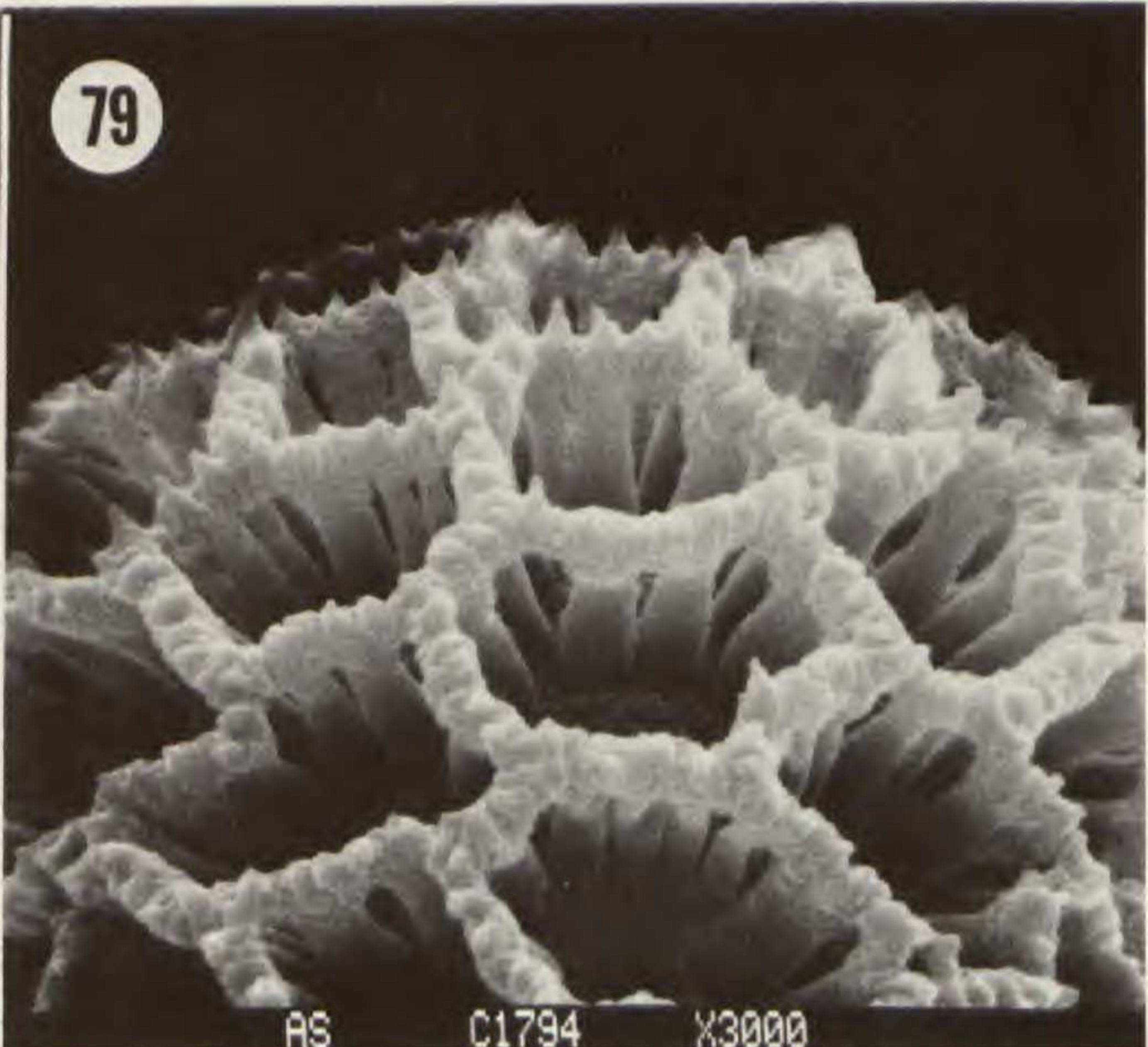
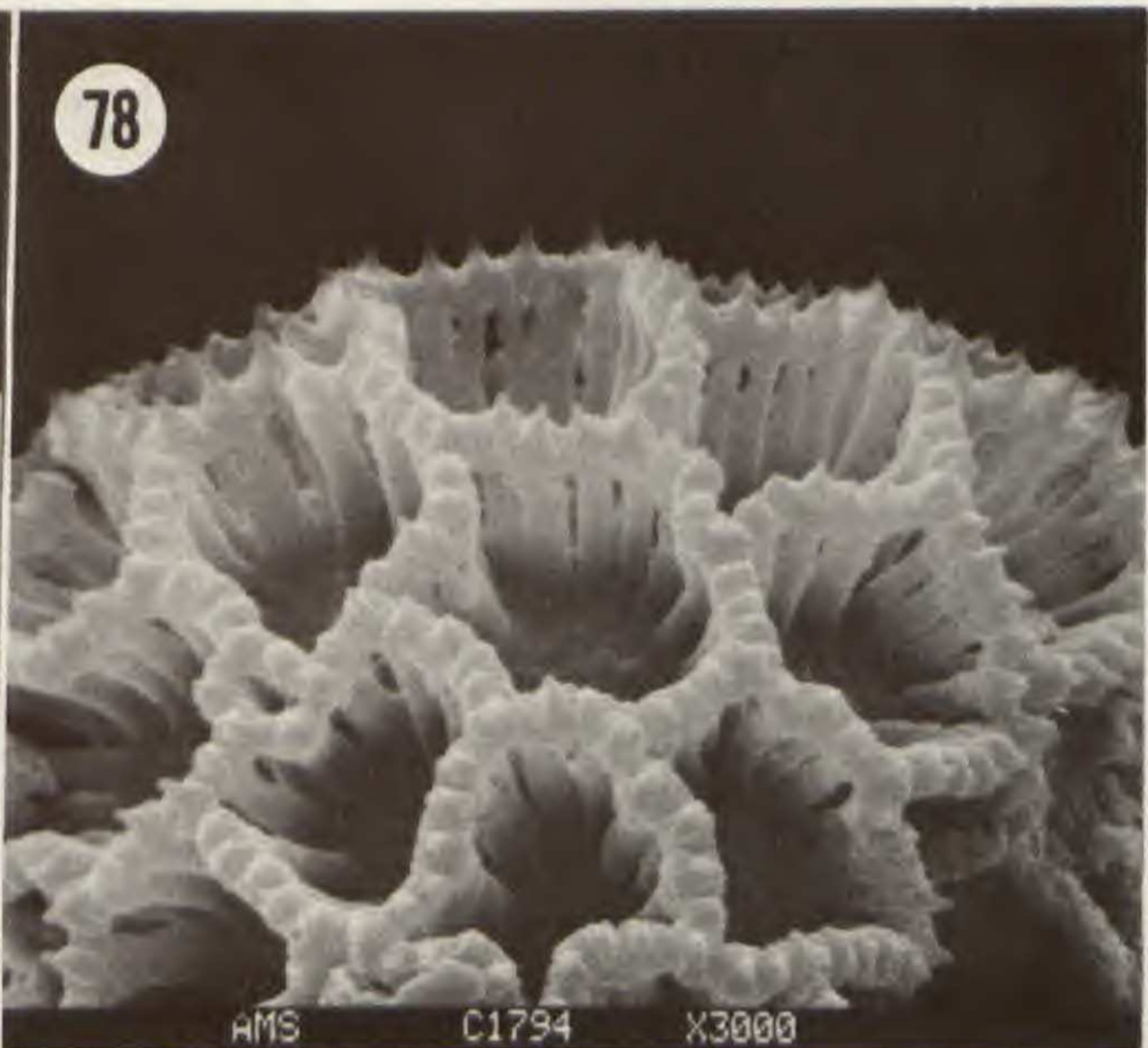
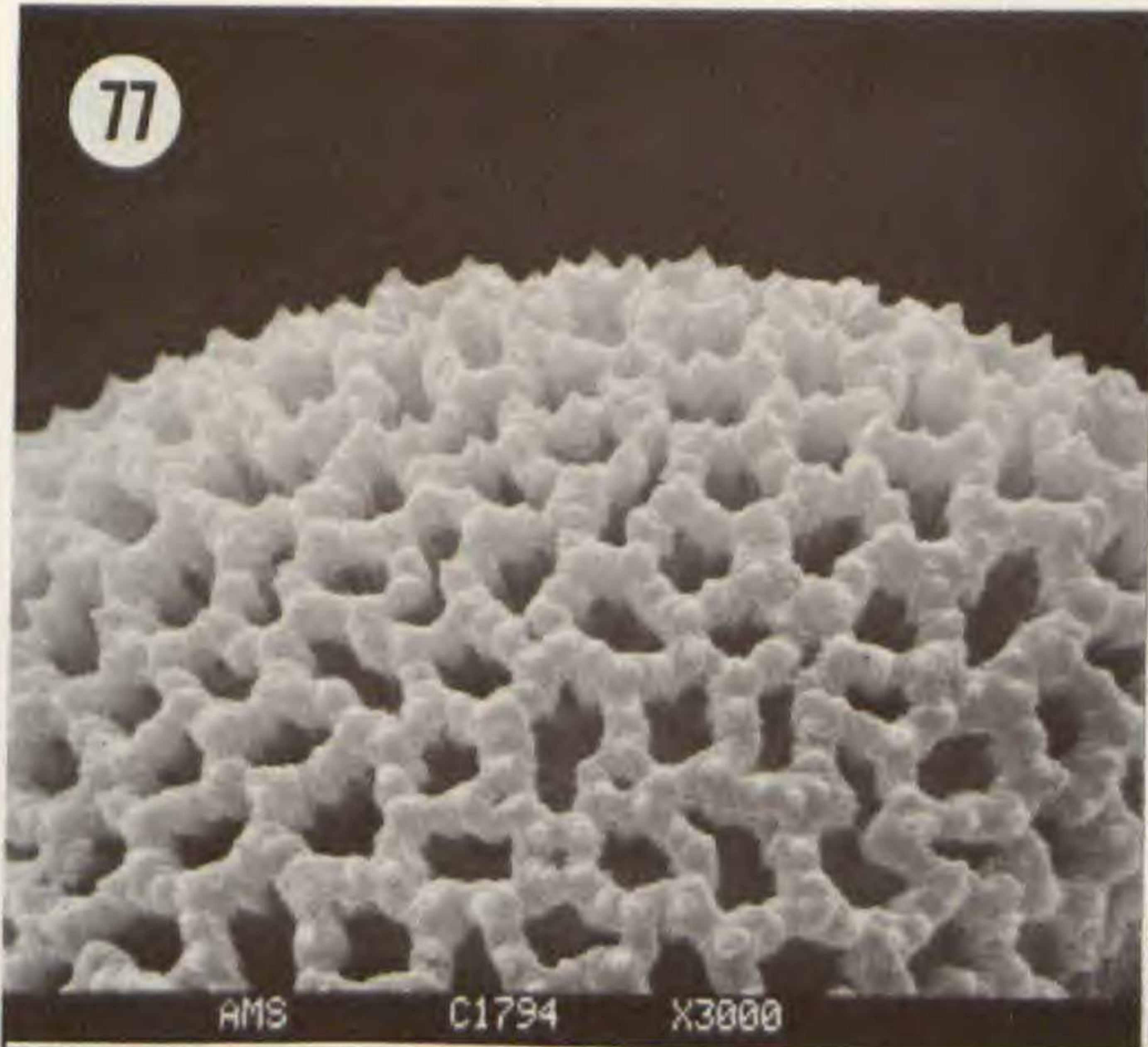
The Batidaceae consists of one genus and two species distributed along the tropical and subtropical littoral, mostly in the New World. Its superficial resemblance to the Chenopodiaceae, wiry stems, succulent leaves, small flowers, and its occupation of a similar habitat, probably initiated the idea of a relationship with the Centrospermae.

The Gyrostemonaceae, 5 genera and perhaps 20 species, is a family of small trees and shrubs endemic to Australia. The superficial resemblance of its female flowers to the free-carpelled members of the Phytolaccaceae may have prompted the early treatment as members of that family.

The dubious relationship between the Batidaceae and Gyrostemonaceae, seemingly initiated by their mutual inclusion and exclusion from the Centrospermae, received unwarranted support when transmission electron microscopy revealed an unstratified exine in each family (Figs. 65–70). The structure of the exine distinguishes the Gyrostemonaceae from all other dicots that have been examined in thin section. As illustrated in Figs. 65–68, the ectexine is unstratified and lacks the typical components, foot layer, columellae, and tectum. There are, however, certain characteristics which deserve mention: in the mesocolpus, Figs. 66 and 68, the endexine (nexine of Prijanto, 1970a) is thin and of a uniform

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FIGURES 71–76. Scanning Electron Micrographs of Plumbaginaceae pollen.—71. *Ceratostigma griffithii* C. B. Clarke, polar view, pointed verrucae form,  $\times 990$ .—72. *C. griffithii*, ectexine surface,  $\times 3,550$ .—73. *C. griffithii*, equatorial view, rounded verrucae form,  $\times 890$ .—74. *C. griffithii*, ectexine surface,  $\times 3,550$ .—75. *Statice tenella* Turcz., equatorial view, coarsely reticulate form,  $\times 1,140$ .—76. *S. tenella*, polar view, finely reticulate form,  $\times 1,100$ .



density, whereas in the region of the colpus, Fig. 67, it is massive due mostly to an additional substance which is less electron dense; the ectexine is for the most part amorphous, but the extreme distal portion may be an exception, and the proximal part does have small, vertical elements distinguished by a greater electron density. These characteristics, although subtle, essentially agree with the earlier work of Prijanto (1970a).

In SEM all Gyrostemonaceae examined (Nowicke, 1975: figs. 67–69; Goldblatt et al., 1976: figs. 1A–1C; Behnke, 1977: figs. 10–14) are similar in aperture, 3-colpate with well-delimited colpi, and in the exine surface which varies only slightly from the psilate condition, e.g., *Gyrostemon australasicus*, Fig. 62, *Codonocarpus attenuatus*, Fig. 63, and *Didymotheca pleiococca*, Fig. 64.

Figure 61 is, to our knowledge, the first SEM of *Batis maritima* and illustrates an almost psilate (finely granular?) surface and a 3-colporoidate aperture condition.

Only one collection of *Batis maritima* (Table 1) was examined in thin section, Figs. 69–70, and the subtle differences found in the exine of Gyrostemonaceae were not apparent. These results agree with those of Prijanto (1970b).

Other similarities in pollen morphology between the two families include the aperture condition, 3-colpate or 3-colporoidate, and a psilate or granular exine surface. These characteristics are common in the dicots and their mutual presence does not, a priori, indicate a relationship, but they do not argue against one.

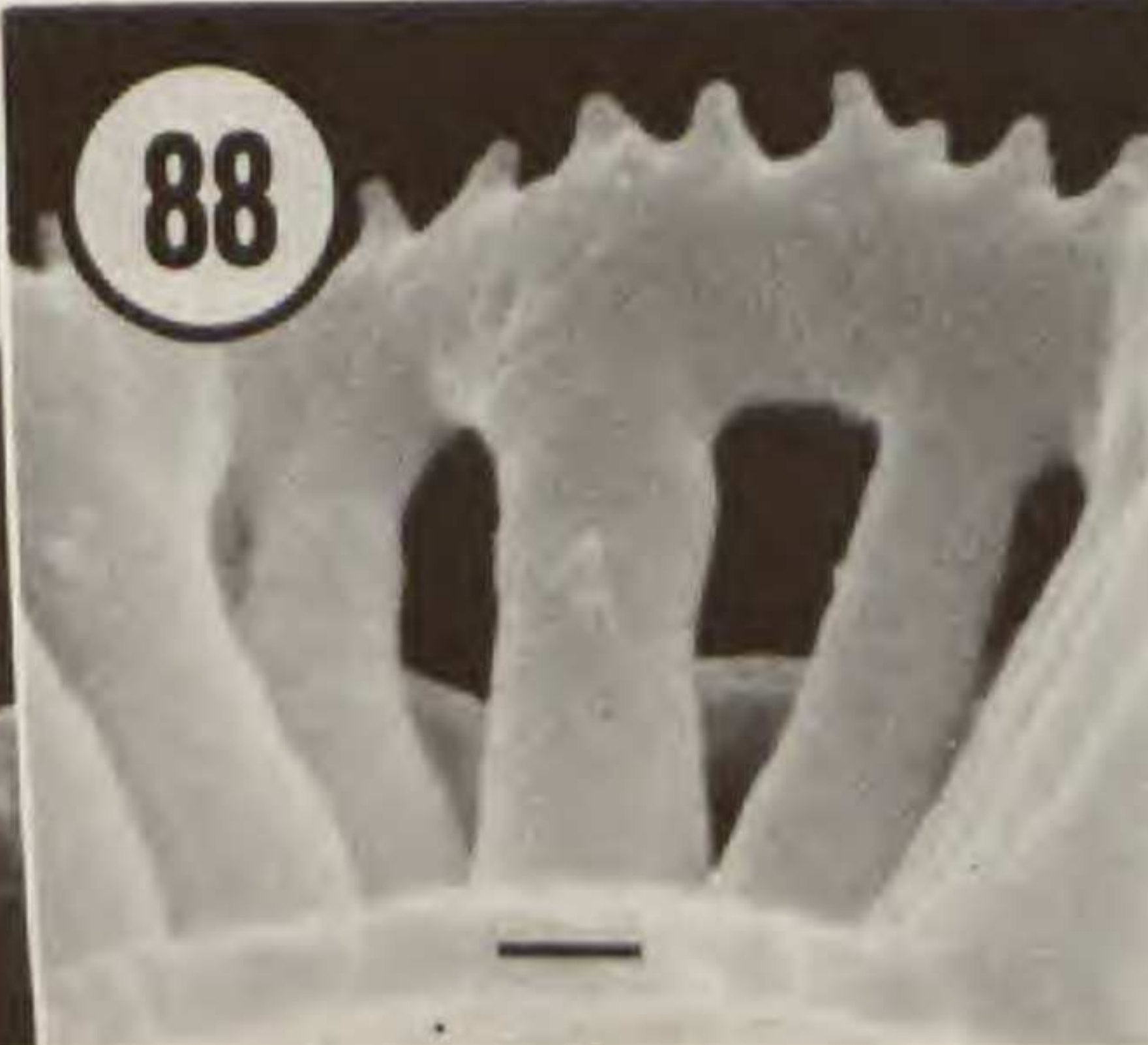
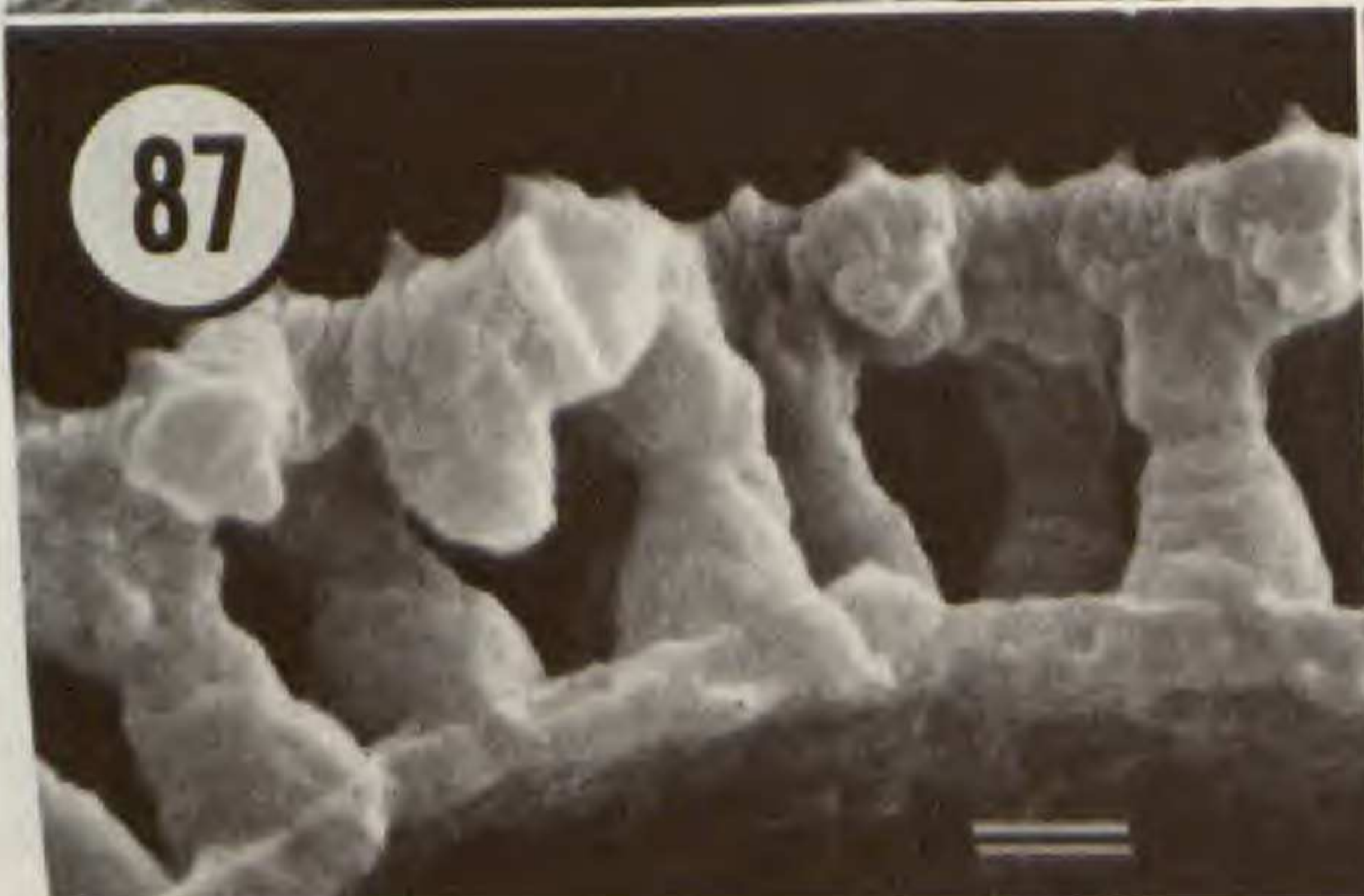
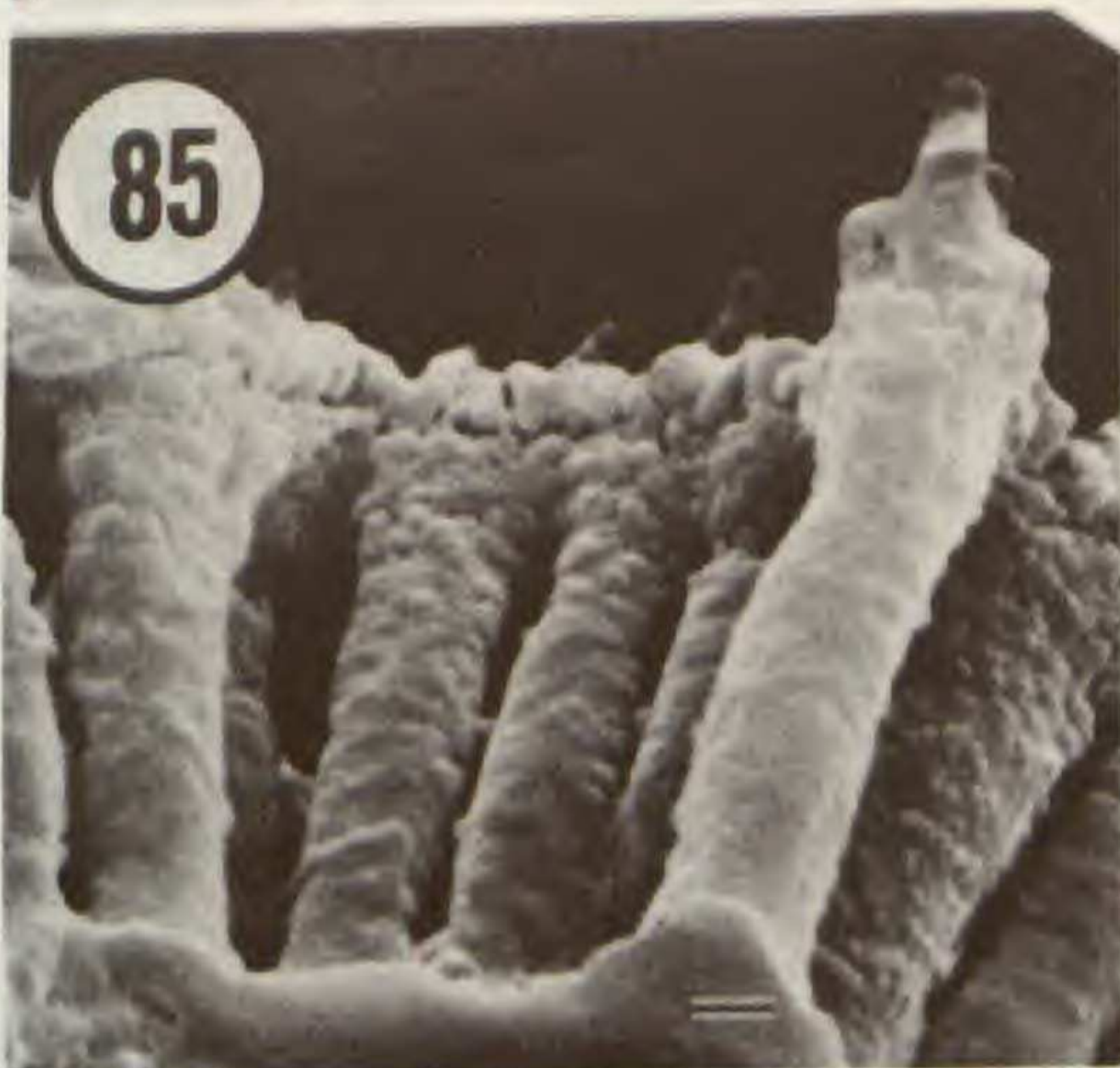
According to Eckhardt (1971) there are similarities in the inflorescences, and Mabry (1976) has reported the presence of glucosinolates in both families. The Batidaceae and Gyrostemonaceae have in common another characteristic more rare than the unstratified exine, and that is the absence of pigmented parts. These two families have neither anthocyanins nor betalains, a condition not found in the remaining dicots, to our knowledge.

There are striking differences between the two families: the Batidaceae are wiry herbs with opposite leaves, have female flowers consisting of two carpels, and seeds with a straight embryo and no endosperm; in contrast, the Gyrostemonaceae are shrubs or trees with alternate leaves, the female flowers have numerous carpels attached to a central column, seeds with a curved embryo and copious endosperm.

In view of the unusual similarities, it seems unwise to summarily dismiss the possibility of a relationship between the Batidaceae and Gyrostemonaceae. A reexamination of the floral and vegetative morphology of both families might clarify their relationship to each other and their position in the dicot hierarchy. Thorne's (1976) suggestion that the Gyrostemonaceae may be related to the wind-pollinated Australian Sapindaceae should be explored, since *Dodonaea* (unpublished data) has thick-walled grains. The male and female flowers in the Gyrostemonaceae do not have the characteristics or modifications associated with wind pollination.

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FIGURES 77–82. Scanning Electron Micrographs of the variation in the tectum of *Armeria maritima* var. *sibirica* (Turcz.) Lawrence (Plumbaginaceae), all  $\times 2,010$ .—77–79. All from one inflorescence (Cody 1794 US, Greenland).—80–82. All from one inflorescence (Calder 2014 US, Canada). The identification system (alpha numerics) has been retained in Figs. 77–82.



## THE ORDERS PLUMBAGINALES, POLYGONALES AND PRIMULALES

The accumulating data on the limited distribution of the betalains and the specialized protein type of sieve-tube plastid, as well as the close similarity of the pollen morphology, strongly suggest that the Centrospermae are a terminal group in the dicots. We believe that the ancestral stock of the Centrospermae separated very early from the main group of dicot predecessors, and that this line gave rise to only the cluster of betalain families and Caryophyllaceae and Molluginaceae, and to no other existing angiosperms. Despite the presence of the anthocyanins and the starch type sieve-tube plastid and the absence of perisperm storage tissue and curved embryo, the Polygonaceae, and to a lesser extent the Plumbaginaceae, are considered to be related to or derived from the Centrospermae. These two families, as well as the Primulaceae which has a free central placentation in common with the Centrospermae, formed the subject matter for the third study, "Pollen Morphology and the Relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the Order Centrospermae" (Nowicke & Skvarla, 1977). In a comprehensive study that combined and integrated SEM and TEM, the pollen of 134 species in these three families was examined. The authors' conclusions, that the Plumbaginaceae, Polygonaceae, and Primulaceae are not related to nor derived from the Centrospermae, and that the three families are not related to each other, are documented with an extensive series of electron micrographs.

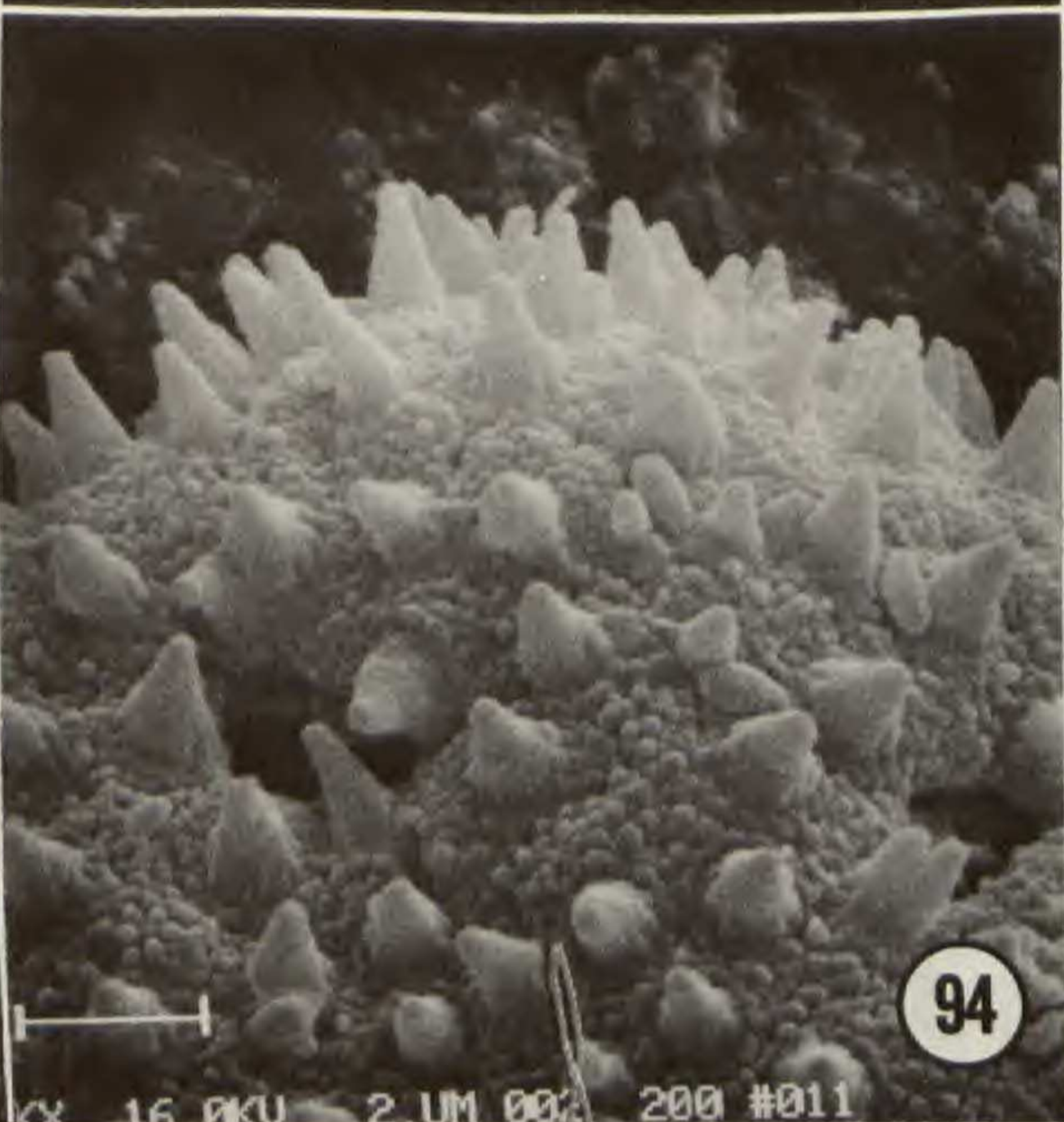
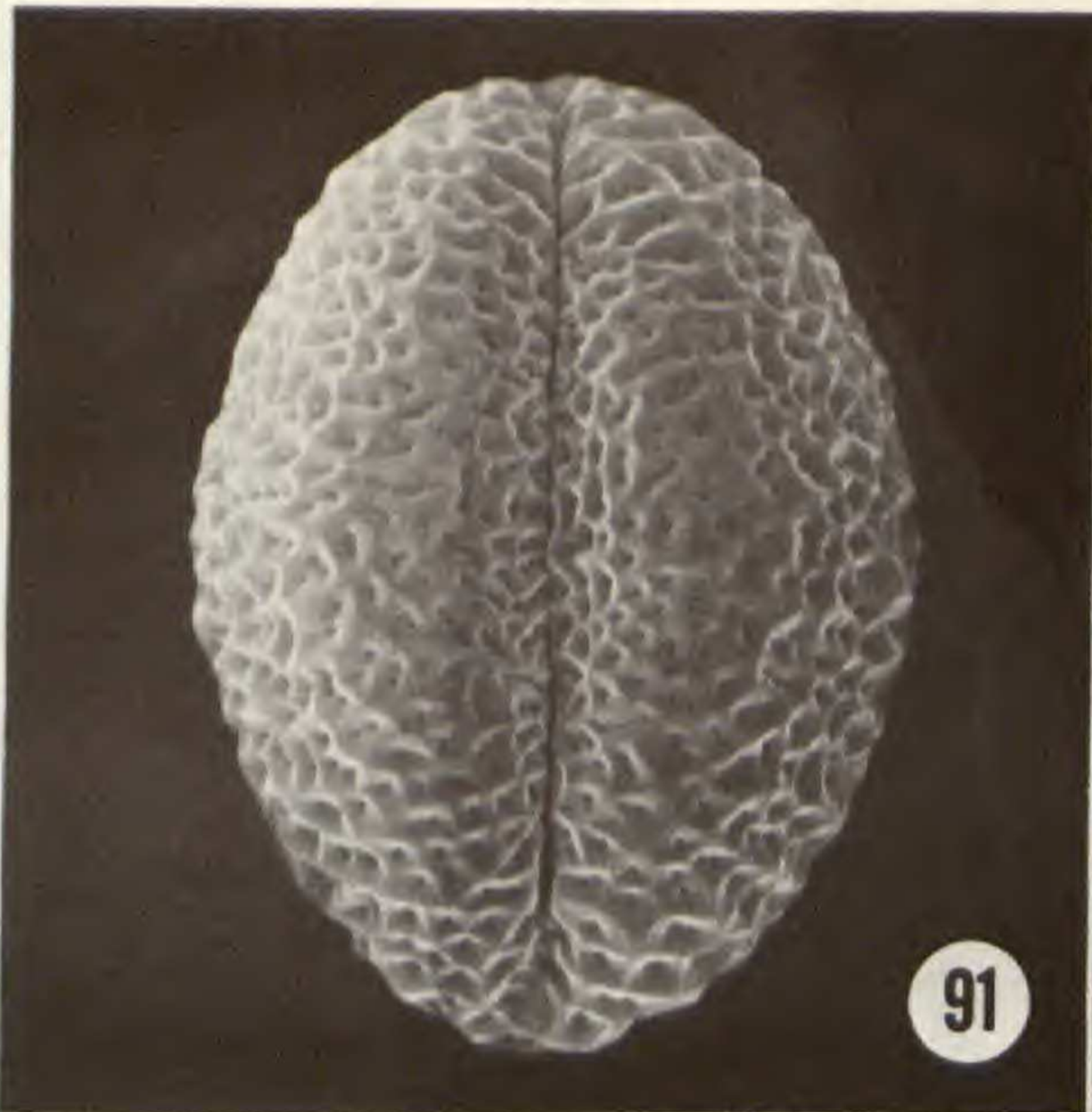
## PLUMBAGINACEAE

The Plumbaginaceae has only two pollen types which Erdtman (1966) designated as the *Armeria* type and the *Plumbago* type, presumably for the genera in which he first found them. The most significant result in a systematic sense is the magnitude of the distinction between the two types: the *Armeria* type grains, Figs. 75–88, are 3-colpate, the tectum incomplete and of a reticulate configuration, the muri consist of a single row of columellae, the lumina represented by the foot layer, and lack free columellae (Nowicke & Skvarla, 1977: figs. 41–58, 65–68, 73–75, 77–81); the *Plumbago* type grains, Figs. 71–74, 89–90, are 3-colpate, rarely pantocolpate, the tectum complete, supporting verrucae placed singly or in small clusters (Nowicke & Skvarla, 1977: figs. 29–40, 59–64, 69–72, 76).

In TEM the difference appears muted, but the structural difference is just as significant if not more so than the exomorphology illustrated in SEM: the *Plumbago* type has a tectum which is complete, Figs. 89–90, while the tectum in the *Armeria* type, Figs. 83–88, consists only of the distal fusion of the sparsely placed columellae. In thin section the *Plumbago* type has a foot layer, columellae, and

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FIGURES 83–90. Transmission Electron Micrographs and Scanning Electron Micrographs of Plumbaginaceae pollen.—83. *Armeria maritima* (Miller) Willd., finely reticulate form,  $\times 5,880$ .—84. *A. maritima*, finely reticulate form, aperture margin,  $\times 6,440$ .—85. *A. maritima*, coarsely reticulate form, SEM of fractured grain,  $\times 3,690$ .—86. *A. maritima*, coarsely reticulate form,  $\times 3,640$ .—87. *Statice sinuata* L., finely reticulate form, SEM of fractured grain,  $\times 6,500$ .—88. *S. sinuata*, coarsely reticulate form, SEM of fractured grain,  $\times 5,000$ .—89. *Ceratostigma griffithii* C. B. Clarke, pointed verrucae form,  $\times 15,080$ .—90. *C. griffithii*, rounded verrucae form,  $\times 10,080$ .

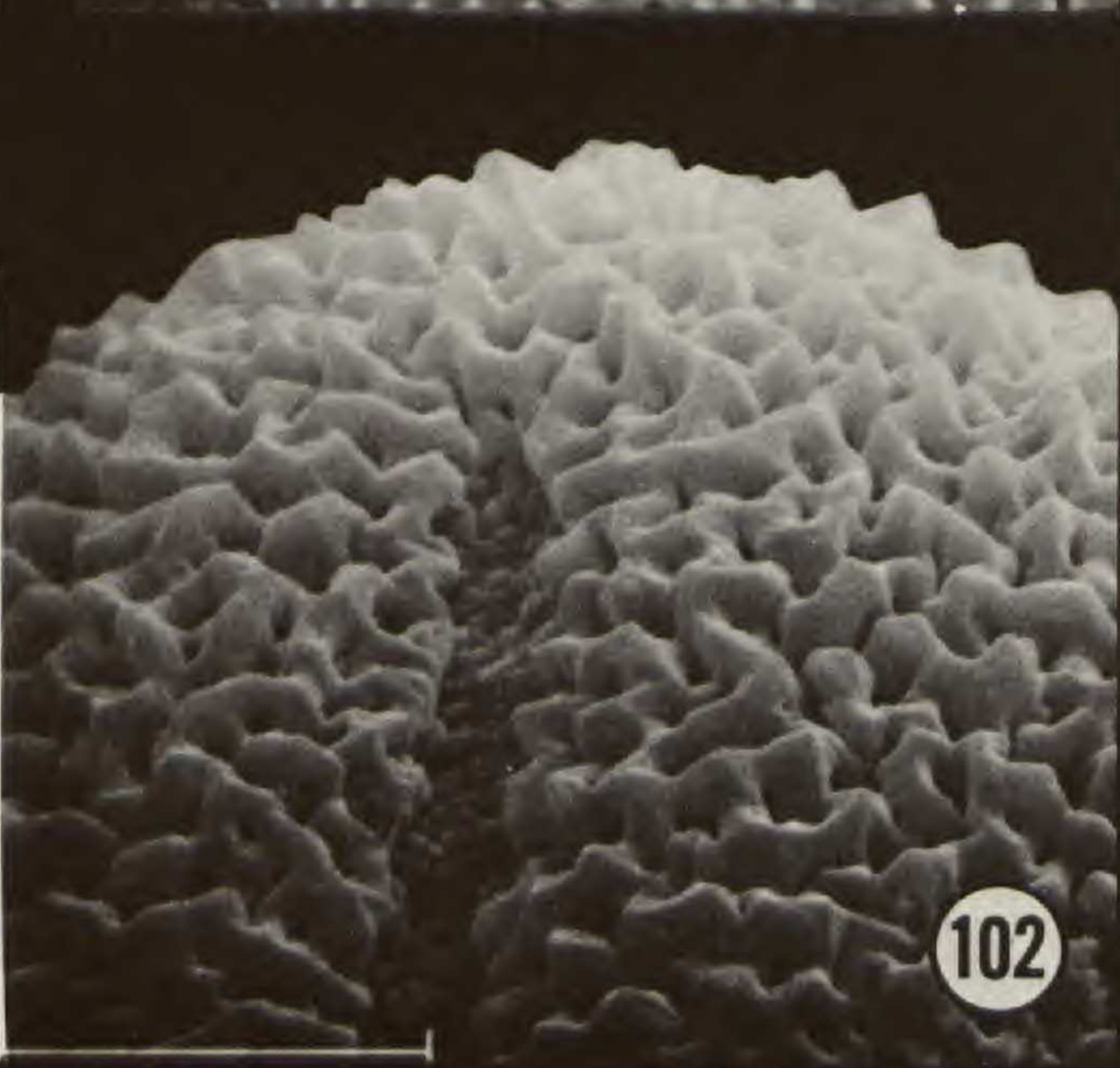
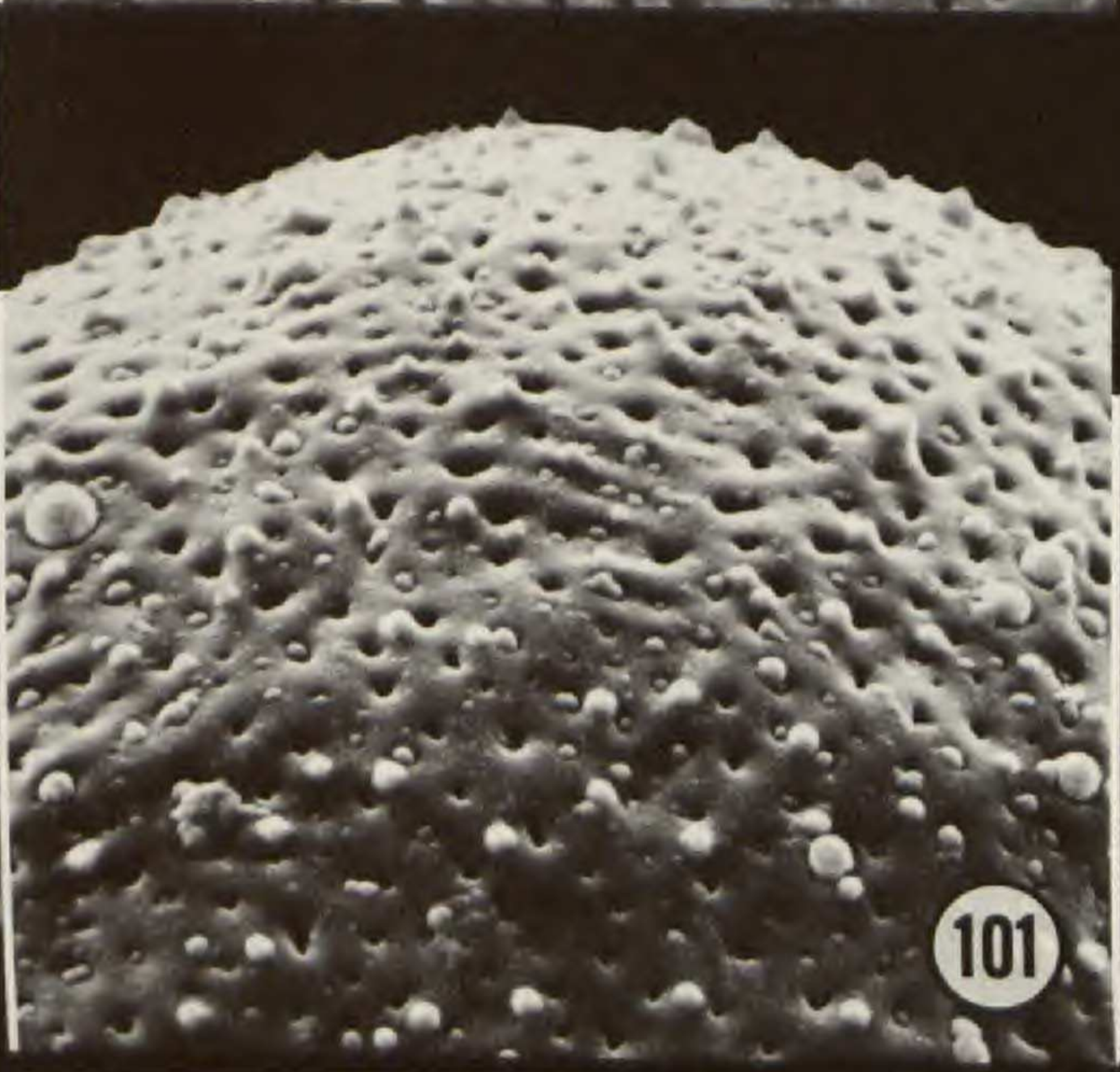
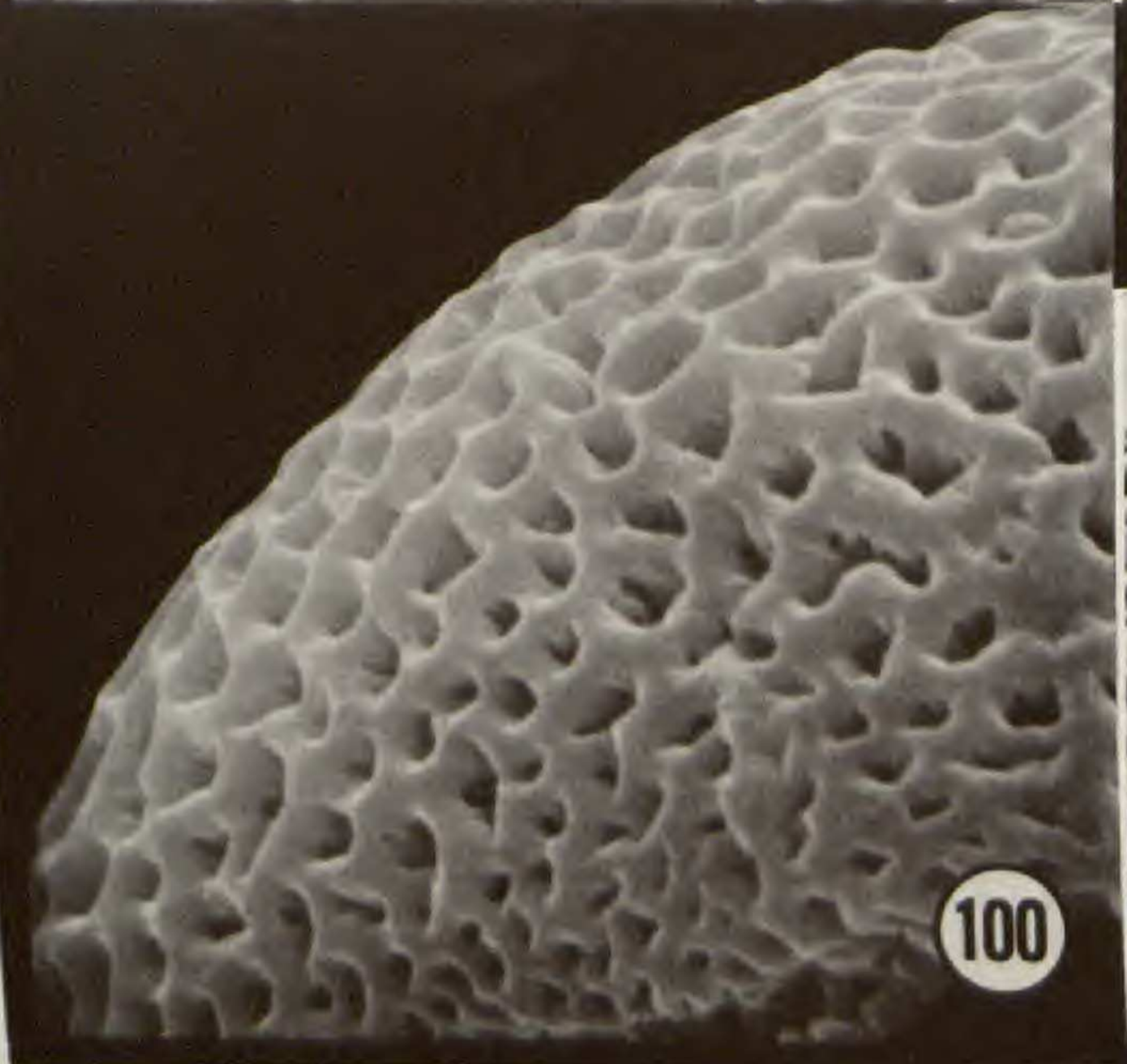
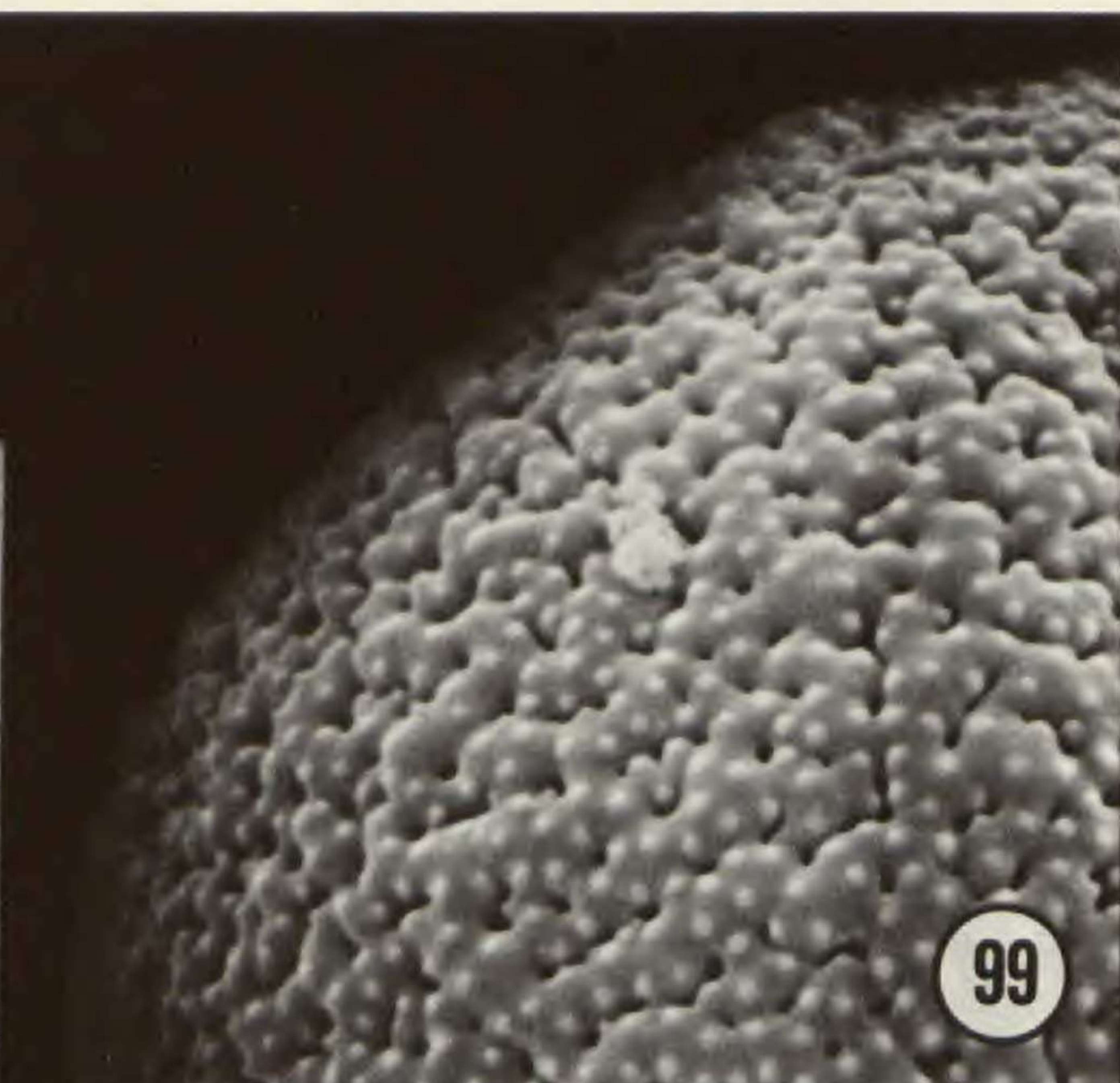
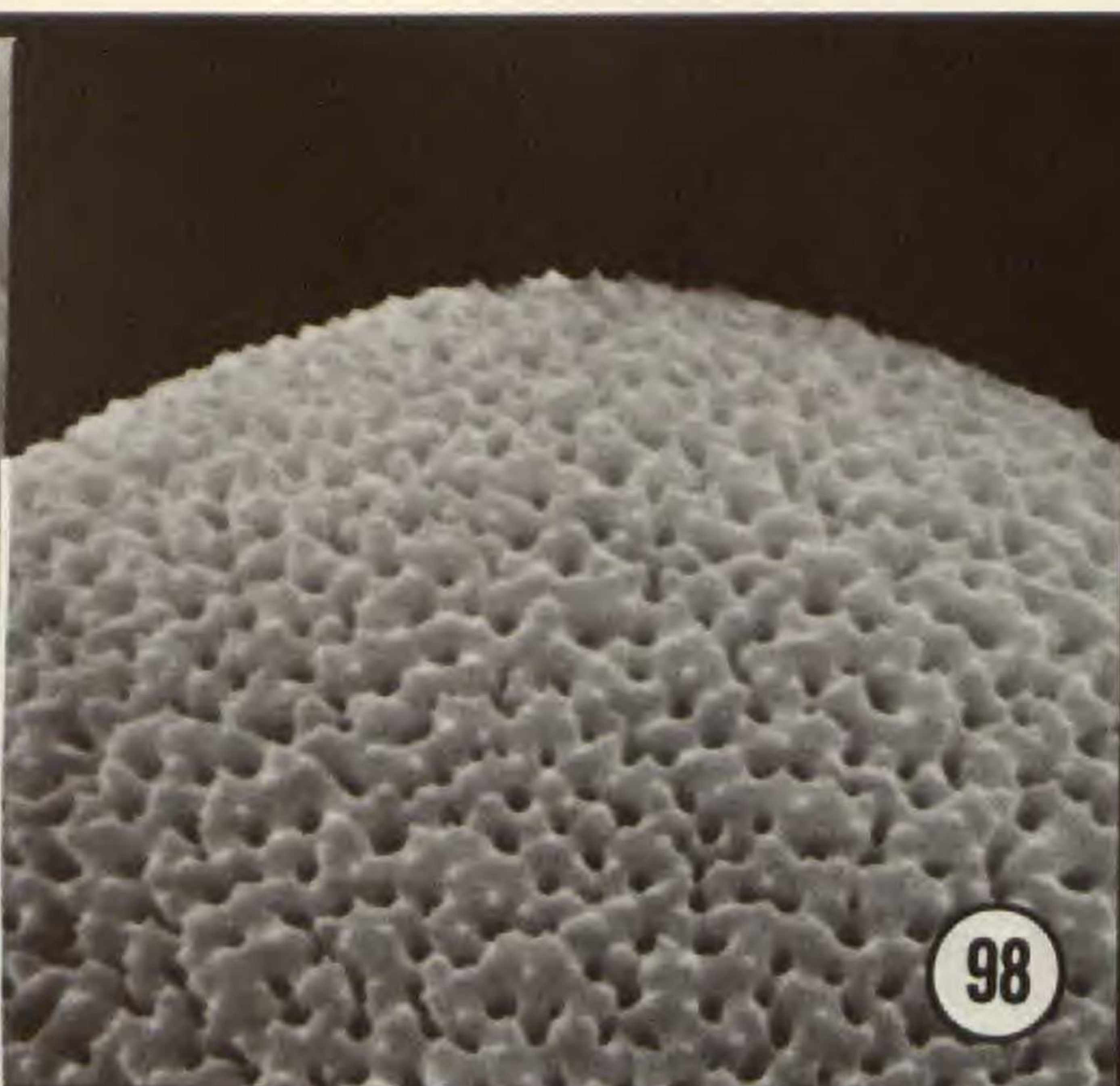
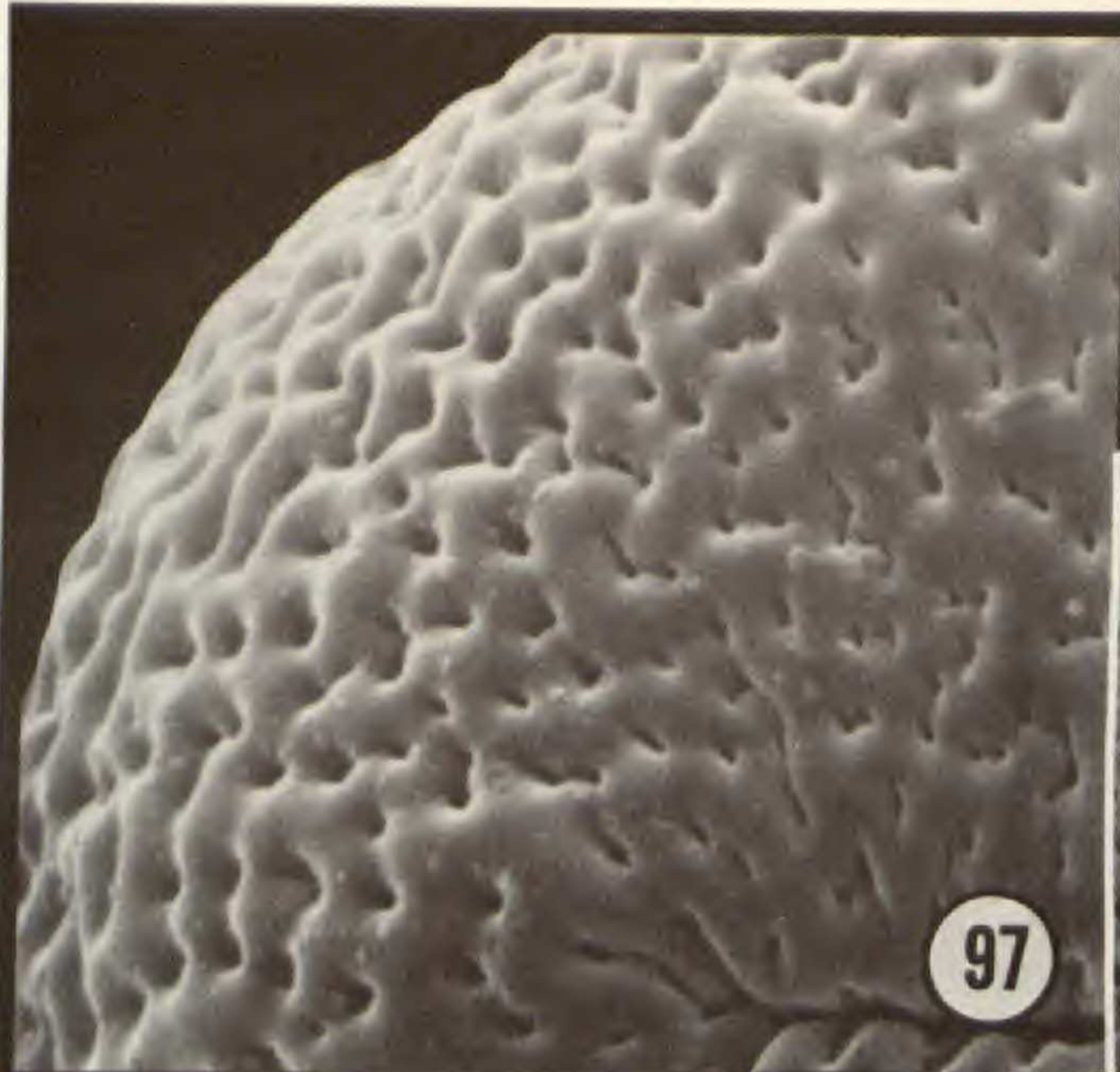


an uneven but continuous tectum (any large gap is an artifact of preparation) on which the verrucae are placed. In contrast, the TEMs of the *Armeria* type illustrate a foot layer, some aspect of the columellae, and some aspect of the tectum, depending on the orientation of the section. With the possible exception of Fig. 84, the thin sections illustrated here do not demonstrate an endexine. Both types do have this layer, at least in the region of the apertures (Nowicke & Skvarla, 1977: figs. 65–66, 68, 71, 73–74, 77, 80–81).

Our interest in the Plumbaginaceae was and is the extent of its relationship to the Centrospermae; nevertheless, we take this opportunity to document an unusual result that was discussed in the previous study (Nowicke & Skvarla, 1977). Each of the two pollen types in the family has two forms: in the *Armeria* type there is a finely reticulate, Figs. 76, 83–84, 87, and a coarsely reticulate, Figs. 75, 85–86, 88, form; in the *Plumbago* type there is a pointed verrucae, Figs. 71–72, 89, and a more rounded verrucae, Figs. 73–74, 90, form. *Armeria maritima* var. *sibirica* has been described as monomorphic (Baker, 1966; Philipp, 1974), i.e., having only one type of stigma and only one form of the *Armeria* type pollen, that with the coarsely reticulate tectum. Using samples only from collections made between longitude 30° West and 60° East, Pragłowski & Erdtman (1969) found six pollen forms, and as many as four in a single anther. Material from this particular geographic region was not available, but we did examine five collections from Greenland and one from Canada (see Table 3, Nowicke & Skvarla, 1977). Anthers were removed from one inflorescence from each collection. All six consisted of mixtures of the finely and coarsely reticulate *Armeria* forms, moreover, the distinction of the two forms was diluted and the coarsely reticulate form was predominant. Figures 77 through 82 illustrate the range of variation found in two of the collections, *Cody 1794* from Greenland, Figs. 77–79, and *Calder 2014* from Canada, Figs. 80–82. All six micrographs were taken at an original magnification of  $\times 3,000$ : in the Greenland collection, Figs. 77 and 79 could be classified as the finely and coarsely reticulate forms, respectively, with Fig. 78 representing only a slight variant of the coarsely reticulate form; on the other hand, the micrographs of three grains from the Canadian collection, Figs. 80–82, are all intermediate in the size of the lumina. Any comments on the origin or adaptive significance of this phenomenon by us would be speculative, and we bequeath the problem to the reproductive strategists and field botanists. The following quote (Nowicke & Skvarla, 1977: p. 8) still applies: "The existence of heterostyly and dimorphic pollen grains in the Plumbaginaceae, however, in no way detracts from the conclusion of this study: None of the pollen examined in the Plumbaginaceae is similar or related to the common type found in the Centrospermae."

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FIGURES 91–96. Scanning Electron Micrographs of Polygonaceae pollen.—91. *Muehlenbeckia polybotryar* Meisn., equatorial view,  $\times 2,230$ .—92. *Fagopyrum cymosum* (Trev.) Meisn., equatorial view,  $\times 1,240$ .—93. *Koenigia islandica* L.,  $\times 2,080$ .—94. *K. islandica*, ectexine surface,  $\times 5,780$ .—95. *Atraphaxis spinosa* L., equatorial view,  $\times 2,590$ .—96. *A. spinosa*, ectexine surface,  $\times 5,780$ . In Figs. 94 and 96 the identification system has been retained, and the magnification bar equals 2  $\mu\text{m}$ .





## POLYGONACEAE

There is almost complete agreement that the Polygonaceae are a well-defined and easily recognized family, the sheathing leaf bases, small trimerous flowers, an undifferentiated perianth, and winged nutlets are easy field markers. Neither the size, 40 genera and 800 species, nor the floral morphology, unspecialized (reduced?), can explain the range of variation in pollen morphology in the Polygonaceae, Figs. 91–124 (Nowicke & Skvarla, 1977: figs. 82–173). The significance of this diversity, especially the origin, is of great interest itself, but for the purpose of this review the conclusion, based on 85 species from the previous study (Nowicke & Skvarla, 1977) and 15 additional species, remains: none of the taxa examined had a pollen morphology similar to the common type in the Centrospermae.

The apertures in the Centrospermae are all simple, whereas in the Polygonaceae compound apertures predominate. In LM the endoapertures are well defined, and the zonorate ones are often strikingly distinct due to the thickened margins. The 3-colporate aperture is the most common type but pantoporate types are also well represented.

The tectum varies widely, from forms which are almost complete or continuous, except for sparsely distributed punctae (Nowicke & Skvarla, 1977: figs. 82, 84), to those in which the tectum is incomplete, represented only by the distal union of major columellae, *Polygonum amphibium*, Fig. 105, *P. orientale*, Fig. 108 (Nowicke & Skvarla, 1977: figs. 112–123). The most common form is punctate-striate, in which the punctae are connected by thin grooves designated as striae, *Muehlenbeckia polybotryar*, Fig. 91, *Fagopyrum cymosum*, Fig. 92, and *Chorizanthe paniculata*, Fig. 97 (Nowicke & Skvarla, 1977: figs. 88–105). In some taxa the striae are longer and deeper, producing an uneven surface consisting of "outpockets" of tectum, as in *Ruprechtia pallida*, Fig. 102, and related species (Nowicke & Skvarla, 1977: figs. 106, 108–109). The tectum of *Podopterus mexicanus*, Fig. 100, has been described as microreticulate, but this designation, like so many others, is an arbitrary one.

In this section all of the taxa examined in the Polygonaceae have the exine stratification considered as typical of the dicots, endexine, foot layer, columellae, and tectum. However, differences in the development of each of these units have produced a variation in the structure of the exine, Figs. 109–124 (Nowicke & Skvarla, 1977: figs. 142–173) that rivals the variation in exomorphology, Figs. 91–108 (Nowicke & Skvarla, 1977: figs. 82–141). The thin sections of *Chorizanthe paniculata*, Fig. 120, *Muehlenbeckia polybotryar*, Fig. 115, and *Ruprechtia pallida*, Fig. 124, can be considered as representative of the most common tectum, punctate-striate (see also Nowicke & Skvarla, 1977: figs. 144–145, 152–153, 171, 173). *Polygonum amphibium*, Fig. 112, and *P. orientale*, Fig. 113, are from taxa with an incomplete or reticulate tectum. Both are radial sections and each illus-

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FIGURES 97–102. Scanning Electron Micrographs of ectexine surfaces of Polygonaceae pollen, all  $\times 5,780$ .—97. *Chorizanthe paniculata* Benth.—98. *Emex australis* Steinheil.—99. *Rumex scutatus* L.—100. *Podopterus mexicanus* H. & B.—101. *Polygonum vacciniifolium* Wall.—102. *Ruprechtia pallida* Standl.



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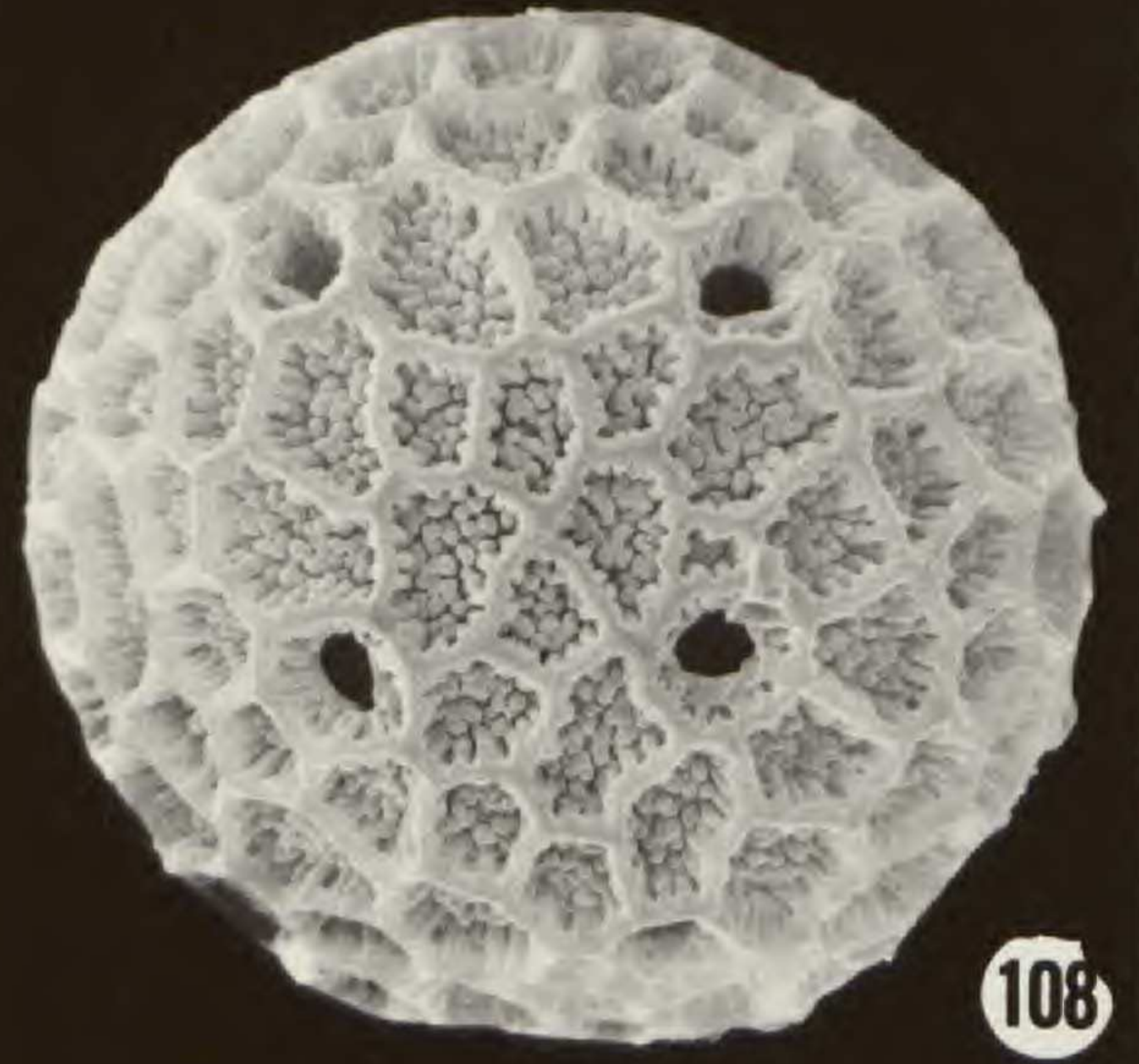
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trates several views of columellae. In Fig. 113, from the pore at the extreme left (note fragment of endexine), the cut is parallel with the long axis of a murus, across a lumina with free columellae, then at a right angle to the long axis of another murus revealing the double row of columellae construction (this is less clear in Fig. 112 due to the slightly oblique angle). The thin section of *Podopterus mexicanus*, Fig. 121, is consistent with the morphology depicted in SEM, Fig. 100. The subfamily Eriogonoideae has a tectum in which the inner surface is granular, illustrated here by *Chorizanthe paniculata*, Fig. 120 (see also Nowicke & Skvarla, 1977: figs. 145–146, 149, 157–158).

The following discussions of specialized morphologies integrate the data from LM, SEM, and TEM.

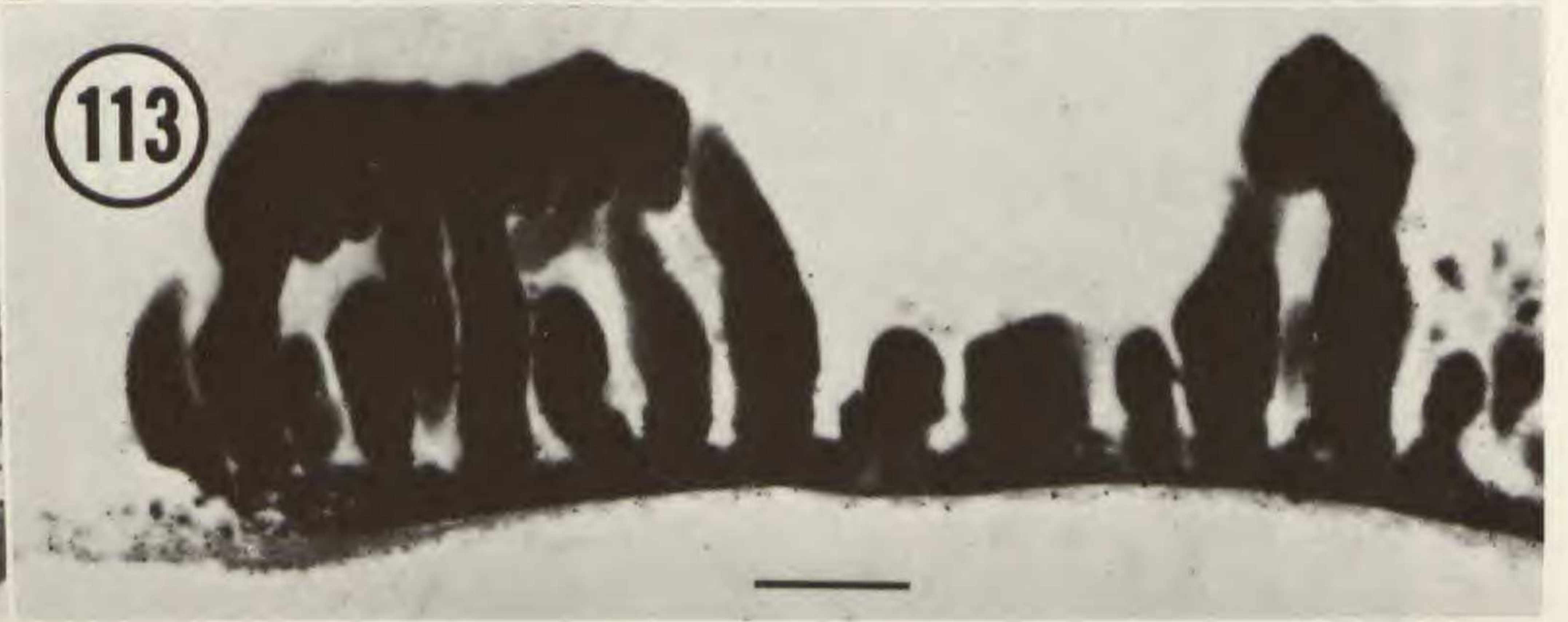
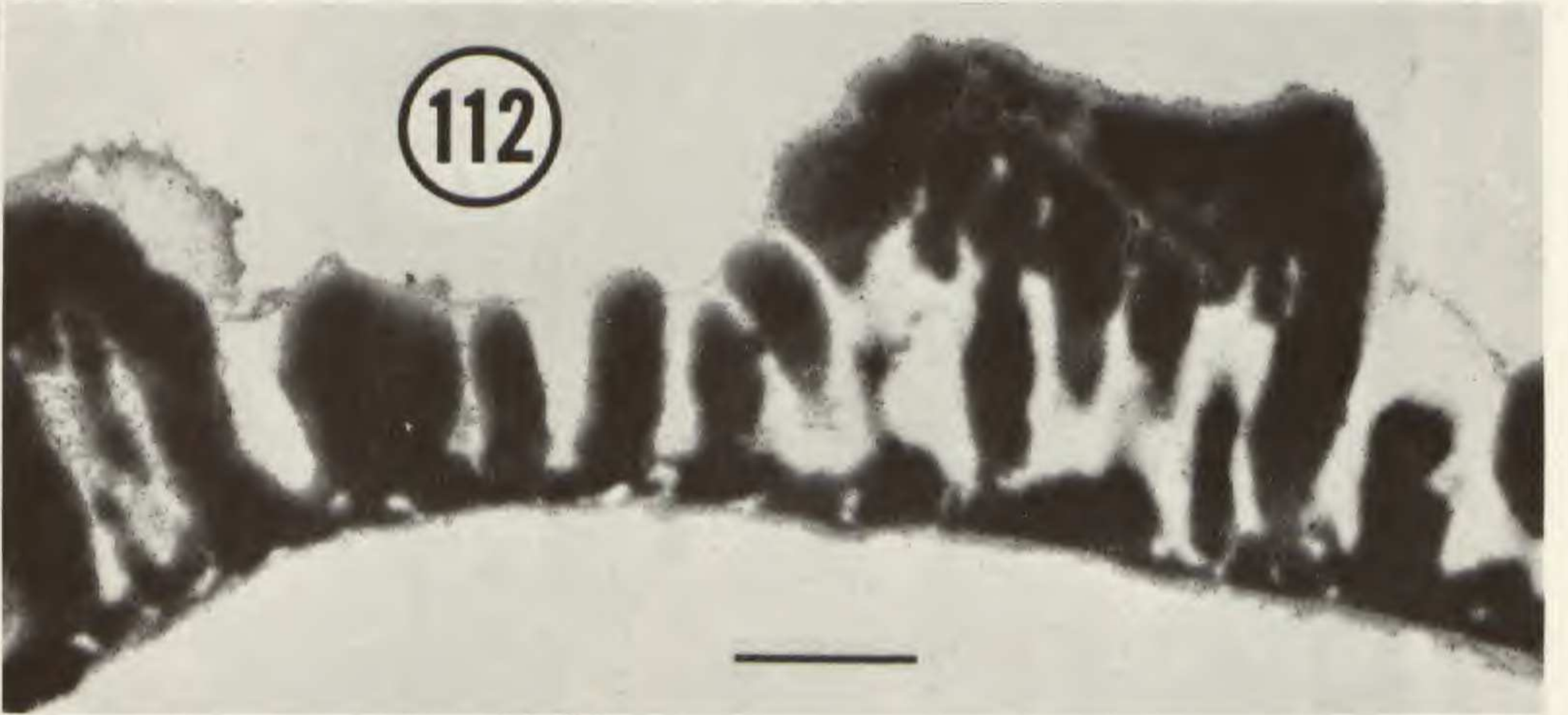
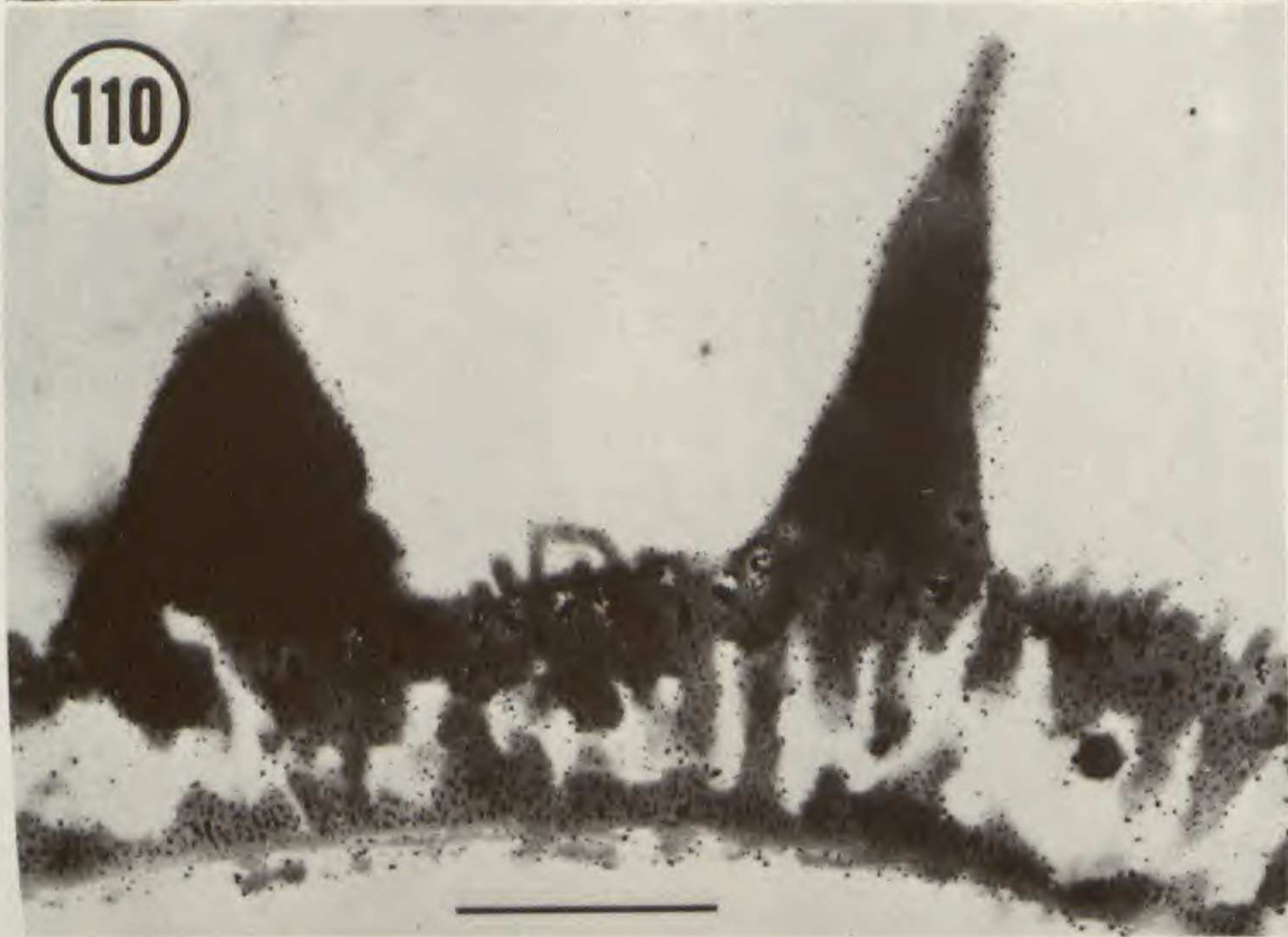
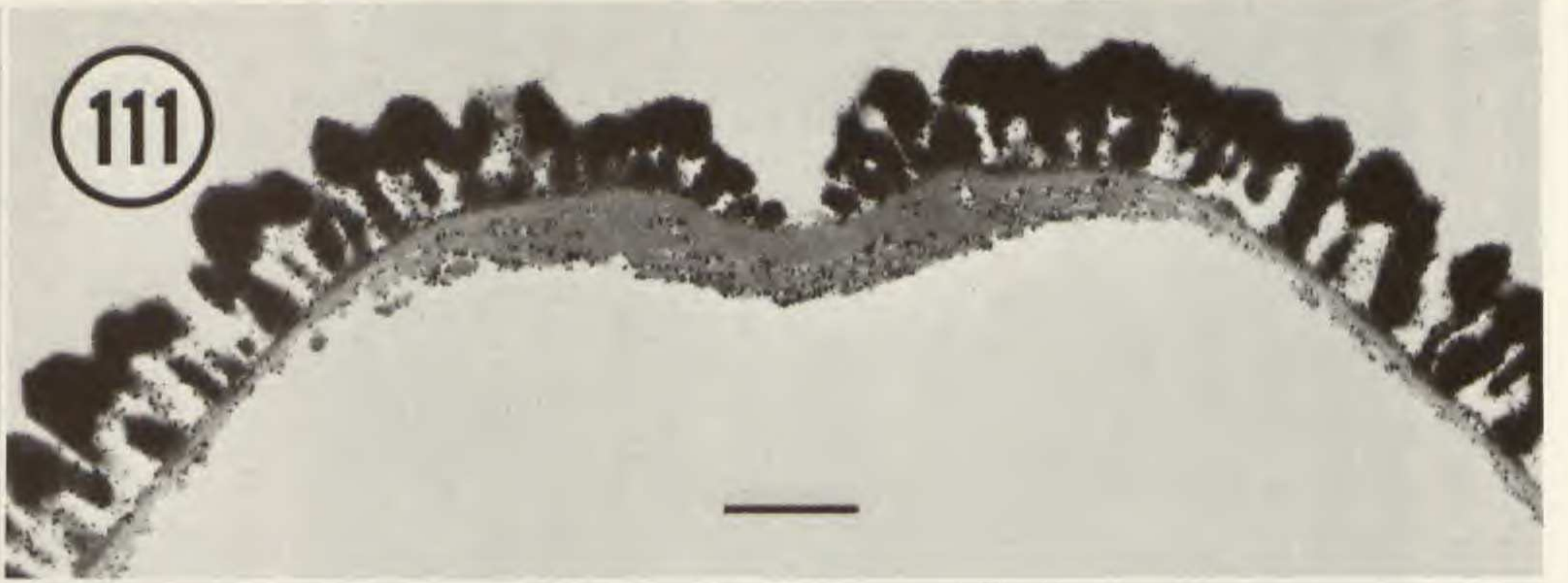
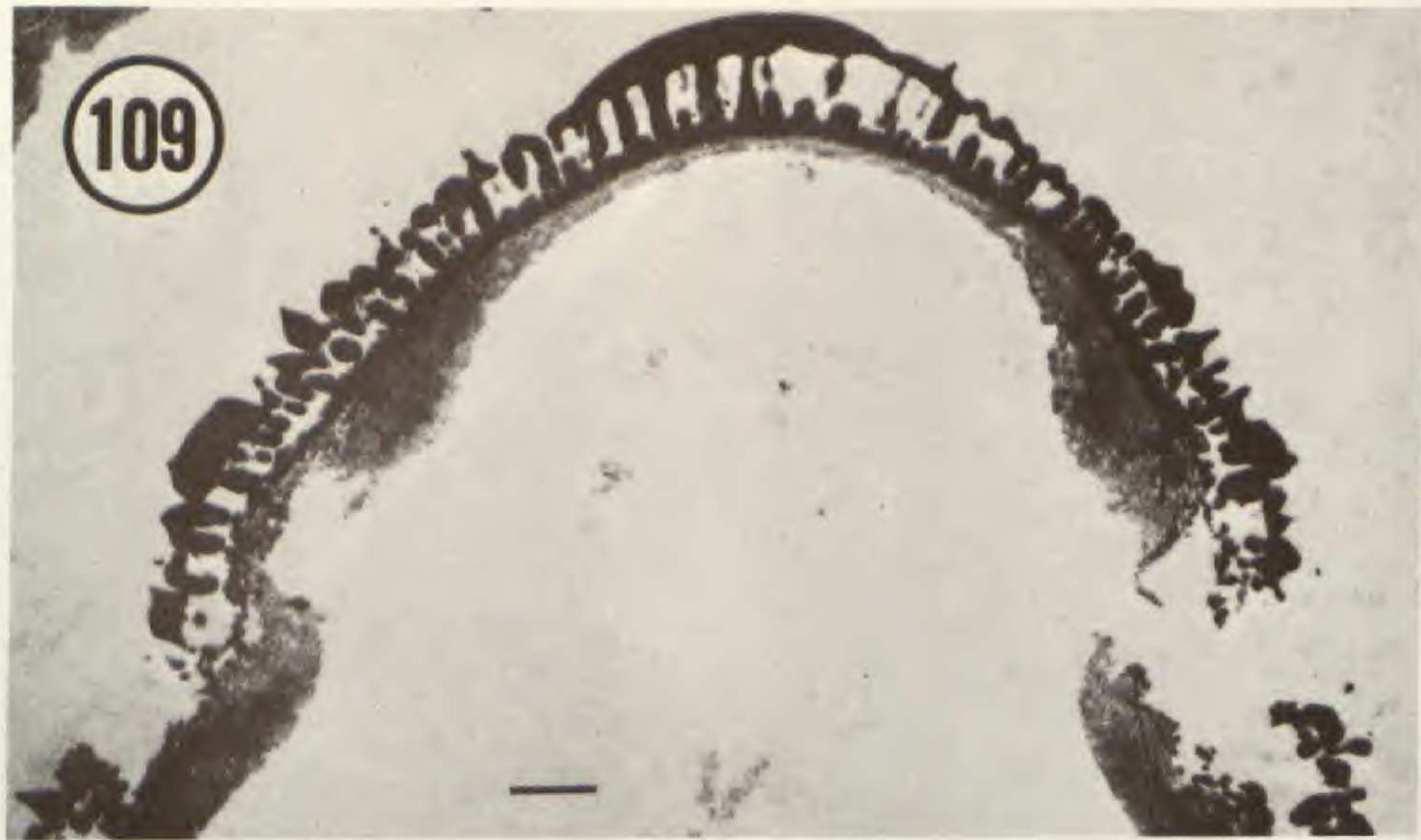
In *Polygonum convolvulus*, Figs. 103 and 109 (Nowicke & Skvarla, 1977: figs. 140–141, 165) and related species, *P. cristatum* and *P. dumetorum*, and also in *Polygonella fimbriata* (Nowicke & Skvarla, 1977: figs. 130, 161) and related species, the tectum is dimorphic: one type outlining the colpi and another type on the mesocolpial ridges and at the poles. Figure 109 is a section at a right angle to the long axis of the grain: the endexine is concentrated mainly under the echinate type which outlines the colpi, and between these two areas is the mesocolpus with the psilate tectum. All of these taxa have a zonorate endoaperture with thickened margins.

Only three species of the approximately 100 examined in this family have pollen with a prominently spinulose tectum: *Koenigia islandica*, Figs. 93–94, 117, *Polygonum forrestii*, Figs. 104, 110 (Nowicke & Skvarla, 1977: figs. 133, 167), and *P. cyanandrium* (Nowicke & Skvarla, 1977: figs. 134–135). *Koenigia* and *P. cyanandrium* are pantoporate but some pores in *Koenigia* grains are distorted; *P. forrestii* is pantocolpate. In thin section, *K. islandica*, Fig. 117, and *P. forrestii*, Fig. 110, are very similar: the spines are the only well-defined component; all others, the foot layer, and especially the columellae, as well as the inner and outer surfaces of the tectum, are irregular and poorly defined. The restricted occurrence of this pollen morphology in the Polygonaceae suggests that these species are closely related (for discussion see Hedberg, 1947).

Only the *Bistorta* complex of *Polygonum*, illustrated here by *P. vaccinifolium*, Fig. 101 (Nowicke & Skvarla, 1977: figs. 124–129) had a tectum which could be described as sparsely spinulose and punctate. The unique structure revealed by thin section, however, dismisses any possibility that these taxa represent a link to the Centrospermae. In Fig. 114, a TEM of *P. vaccinifolium*, the slightly oblique angle detracts from the compacted columellae condition (see also Nowicke & Skvarla, 1977: figs. 164, 168), which distinguishes this group from all other members of the Polygonaceae and from all taxa examined to date in the Centrospermae.

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FIGURES 103–108. Scanning Electron Micrographs of *Polygonum* pollen.—103. *Polygonum convolvulus* L., equatorial view,  $\times 2,240$ .—104. *P. forrestii* Diels,  $\times 2,290$ .—105. *P. amphibium* L.,  $\times 1,160$ .—106. *P. glaciale* (Meisn.) Hook. f., equatorial view,  $\times 1,870$ .—107. *P. cilinode* Michx., polar view,  $\times 2,370$ .—108. *P. orientale* L.,  $\times 1,260$ .



Two genera, *Emex* and *Rumex*, illustrated here by *E. australis*, Fig. 98, and *R. scutatus*, Fig. 99, have a perforate and spinulose tectum in which the spinules are very small and evenly distributed. Comparison of thin sections of *Emex australis*, Figs. 122–123, with those of *Rumex acetosa* (Nowicke & Skvarla, 1977: fig. 170), a thick tectum supported by short, irregular columellae, a questionable foot layer, and an endexine which is exceptionally narrow (except in the aperture, Fig. 123), agrees with the close similarity depicted in SEM, Figs. 98–99, and supports their close relationship on other bases. The remarkably smooth or uniform inner surface of the tectum, Figs. 122–123, is perplexing but the oblique angle of section could, at least in part, produce this effect.

Four of the species examined since the 1977 paper are illustrated here. *Atraphaxis spinosa* has the most conspicuously striate tectum, Figs. 95–96, of all Polygonaceae thus far. In thin section, Figs. 118–119, it is similar to *A. buxifolia* (Nowicke & Skvarla, 1977: fig. 143): both have a well-developed endexine, uneven foot layer, and irregular columellae. *Fagopyrum cymosum*, Fig. 92, is similar to *F. esculentum* (Nowicke & Skvarla, 1977: figs. 87, 150), the latter species is illustrated here in thin section, Fig. 116. *Polygonum cilinode* has a finely punctate-striate tectum, Fig. 107, and is distinguished in thin section, Fig. 111, by the apparent absence of a foot layer. *Polygonum glaciale*, Fig. 106, is from the Asian section *Cephalophilon*, all of which have reticulate ectexines. The size of the pollen and the characteristics of the muri and lumina vary within a sample (Nowicke & Skvarla, unpublished data).

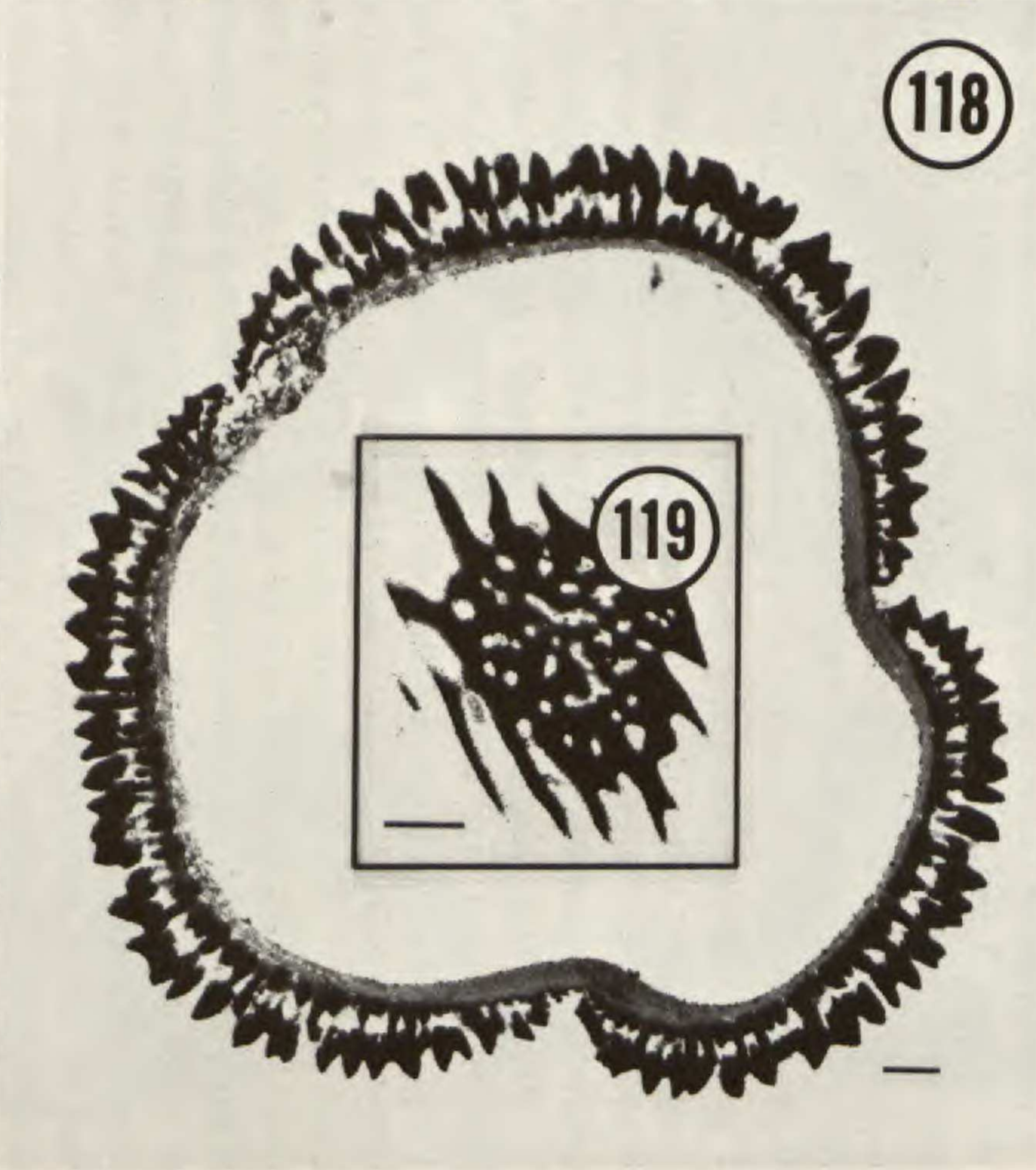
#### PRIMULACEAE

The basis for the relationship between the Primulaceae and the Centrospermae is the presence of free central placentation. However, this similarity is now regarded as an example of parallel evolution or of independent origin, since no other characteristic, including pollen morphology (Nowicke & Skvarla, 1977: figs. 174–200), supports this view. Figures 125–130 could be considered as representative of aperture and tectum variation. *Coris monspeliensis*, Fig. 125, *Anagallis linifolia*, Fig. 126, *Glaux maritima*, Fig. 128, and *Naumbergia thyrsiflora*, Fig. 129, are 3-colpate, while *Cortusa matthioli*, Fig. 127, is a restricted aperture type in which the colpi fuse at the poles forming a triangular apocolpial field. *Primula officinalis*, Fig. 130, is 5–8-zonocolpate. The tectum ranges from finely granular, Fig. 127, to perforate, e.g., Figs. 126, 129, 133. Figure 125 is probably a perforate tectum obscured by a residue of pollenkitt. The lack of agreement in Fig. 128 of *Glaux maritima* with that in an earlier study (Nowicke & Skvarla, 1977: fig. 190) is probably a manifestation of heterostyly and dimorphic pollen (for discussion see Nowicke & Skvarla, 1977).

In thin section most Primulaceae pollen have an identifiable endexine, such as that in *Coris monspeliensis*, Fig. 131, *Glaux maritima*, Fig. 132, *Anagallis*

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FIGURES 109–113. Transmission Electron Micrographs of *Polygonum* pollen.—109. *Polygonum convolvulus* L., ×5,300.—110. *P. forrestii* Diels, ×18,240.—111. *P. cilinode* Michx., ×8,510.—112. *P. amphibium* L., ×11,020.—113. *P. orientale* L., ×9,890.



*linifolia*, Fig. 133, and *Naumbergia thyrsiflora*, Fig. 134. *Cortusa matthioli*, Figs. 135–136, *Primula officinalis*, Fig. 137 (Nowicke & Skvarla, 1977: fig. 198) and *P. veris* (Nowicke & Skvarla, 1977: fig. 200) can be distinguished by the absence of a foot layer and the correspondingly enhanced endexine.

#### THE ORDER RANUNCULALES

The very restricted distribution of both betalains and the protein type sieve tube plastid suggest that the centrospermous ancestors separated from the main stock early in the phylogenetic history of the dicots. If this tenet is accepted, the families which might share a common ancestry are most likely the "lower dicots" and the order Ranunculales is the logical starting point.

Most authors (Cronquist, 1968; Hutchinson, 1959; Takhtajan, 1969; Thorne, 1968) regard the Ranunculales as a primitive or at least unspecialized group of families. For the most part we follow Cronquist's concept of the order which includes the Ranunculaceae, Circaeasteraceae, Berberidaceae, Lardizabalaceae, Menispermaceae, Coriariaceae, Corynocarpaceae, and Sabiaceae.

Unlike the Centrospermae, in which the vast majority of the taxa in the betalain families and in the anthocyanin containing Caryophyllaceae and Molluginaceae had a very similar pollen morphology, the results from this investigation of the order Ranunculales do not support a close relationship between the Ranunculaceae, Berberidaceae, Lardizabalaceae, Coriariaceae, or Corynocarpaceae. (We are aware that a narrow interpretation of the pollen data might well reduce the order Ranunculales to the family Ranunculaceae.)

The discussions of these five families, however briefly presented here, are nonetheless based on examination of almost 200 species. Only the Berberidaceae and Ranunculaceae are illustrated by representative taxa in SEM and TEM.

#### RANUNCULACEAE

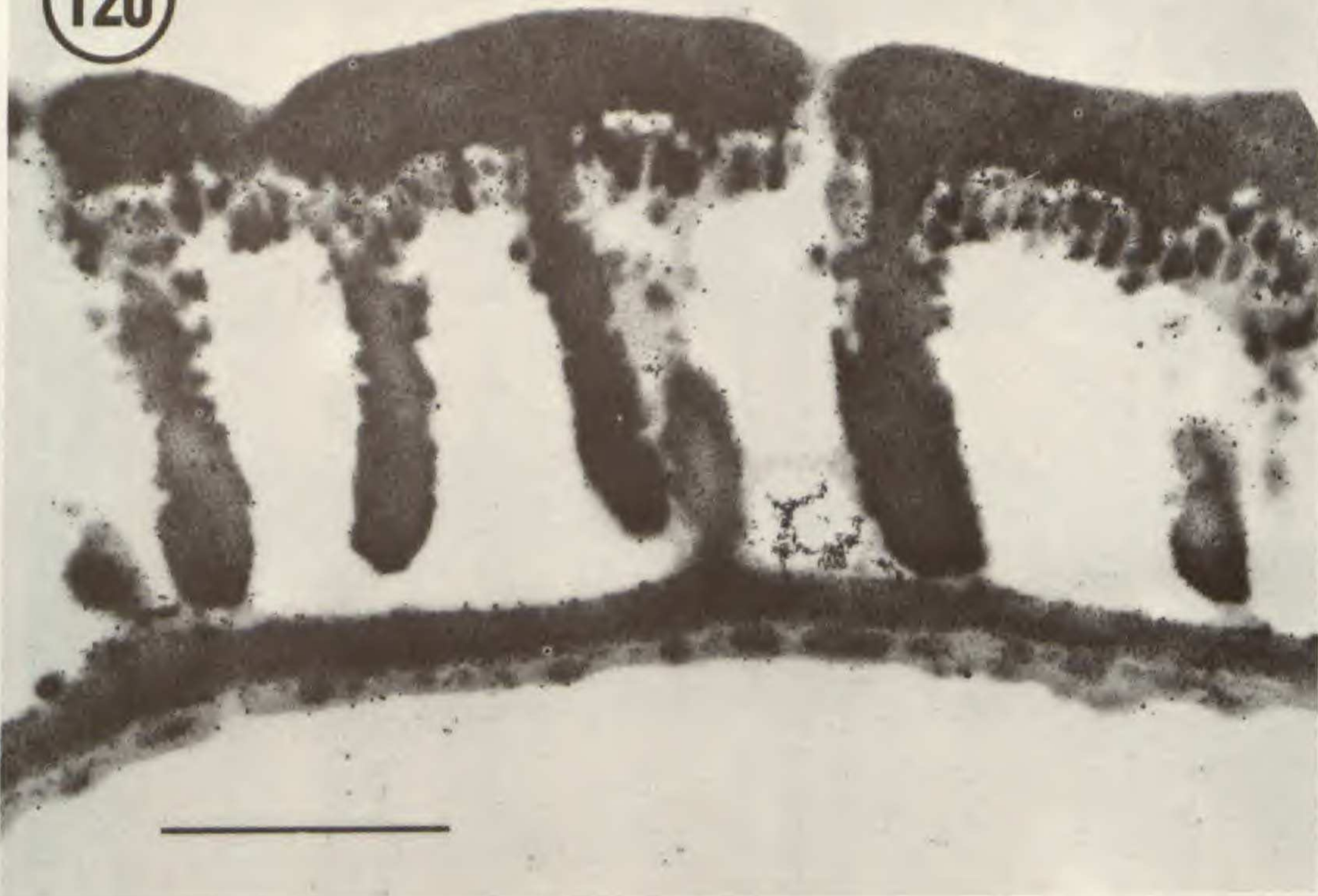
For a large family, 45 to 50 genera and more than 1,000 species, the pollen morphology of the Ranunculaceae is remarkably uniform. Even more remarkable is the fact that the only exceptions to a spinulose and punctate/perforate tectum were found in *Helleborus*, e.g., *H. viridis*, Figs. 164–165, *Hydrastis* (see the following discussion of Berberidaceae), *Paeonia*, e.g., *P. brownii*, Figs. 160–161, and *Trollius* e.g., *T. acaulis*, Figs. 162–163. The first three are controversial genera frequently separated from the Ranunculaceae, and the very distinctive tectum of *Trollius* may well be linked to isolating mechanisms of geographical location and self-fertilization. Certainly these two factors help to maintain this distinction.

All of the remaining taxa examined, 38 genera and 111 species, have a spinulose and perforate tectum. Representative species illustrated in SEM are:

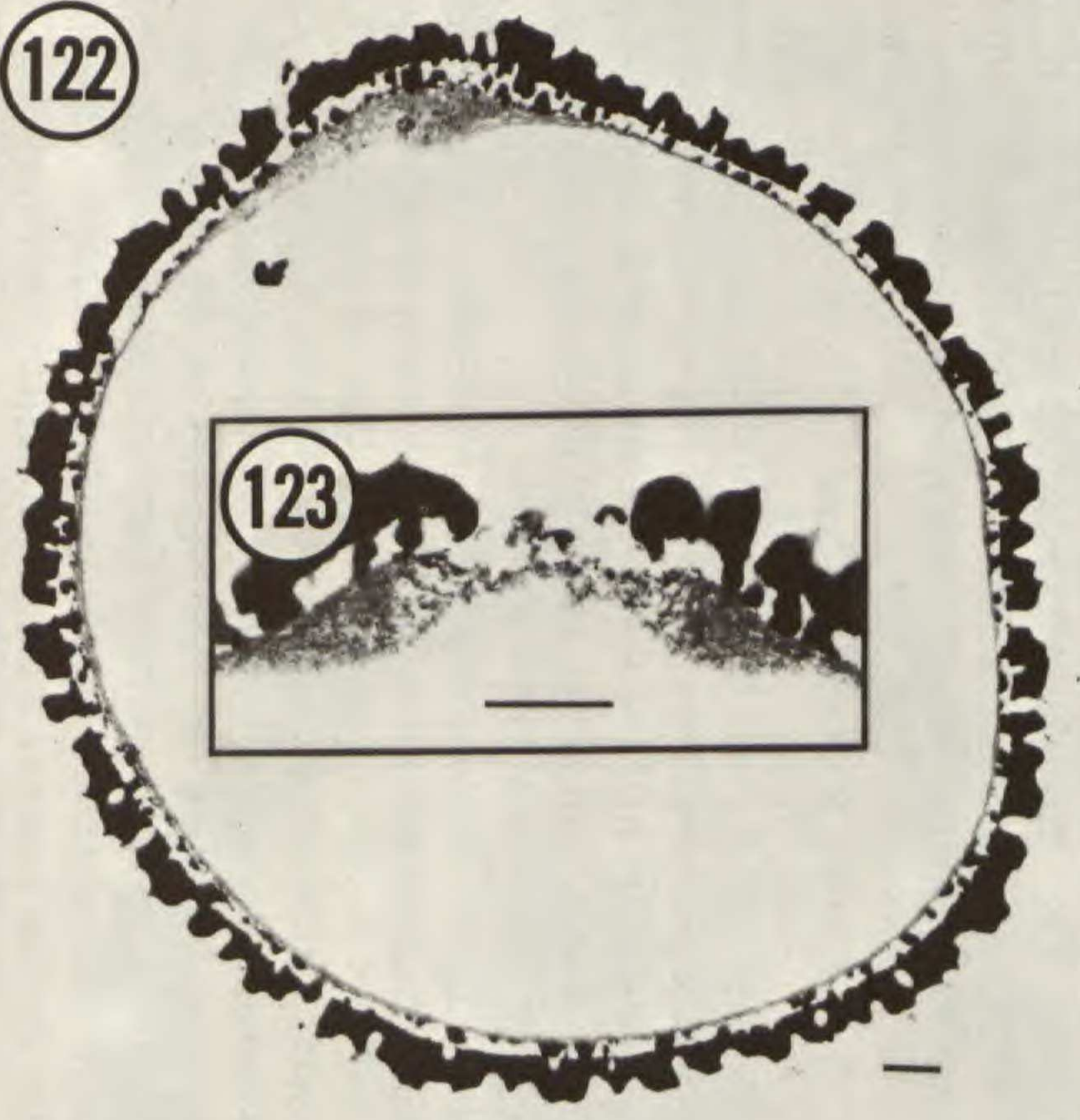
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 FIGURES 114–119. Transmission Electron Micrographs of Polygonaceae pollen.—114. *Polygonum vacciniifolium* Wall., ×13,050.—115. *Muehlenbeckia polybotryar* Meisn., ×13,050.—116. *Fagopyrum esculentum* Moench, ×14,210.—117. *Koenigia islandica* L., ×15,080.—118. *Atraphaxis spinosa* L., ×4,300.—119. *A. spinosa*, ×6,080.

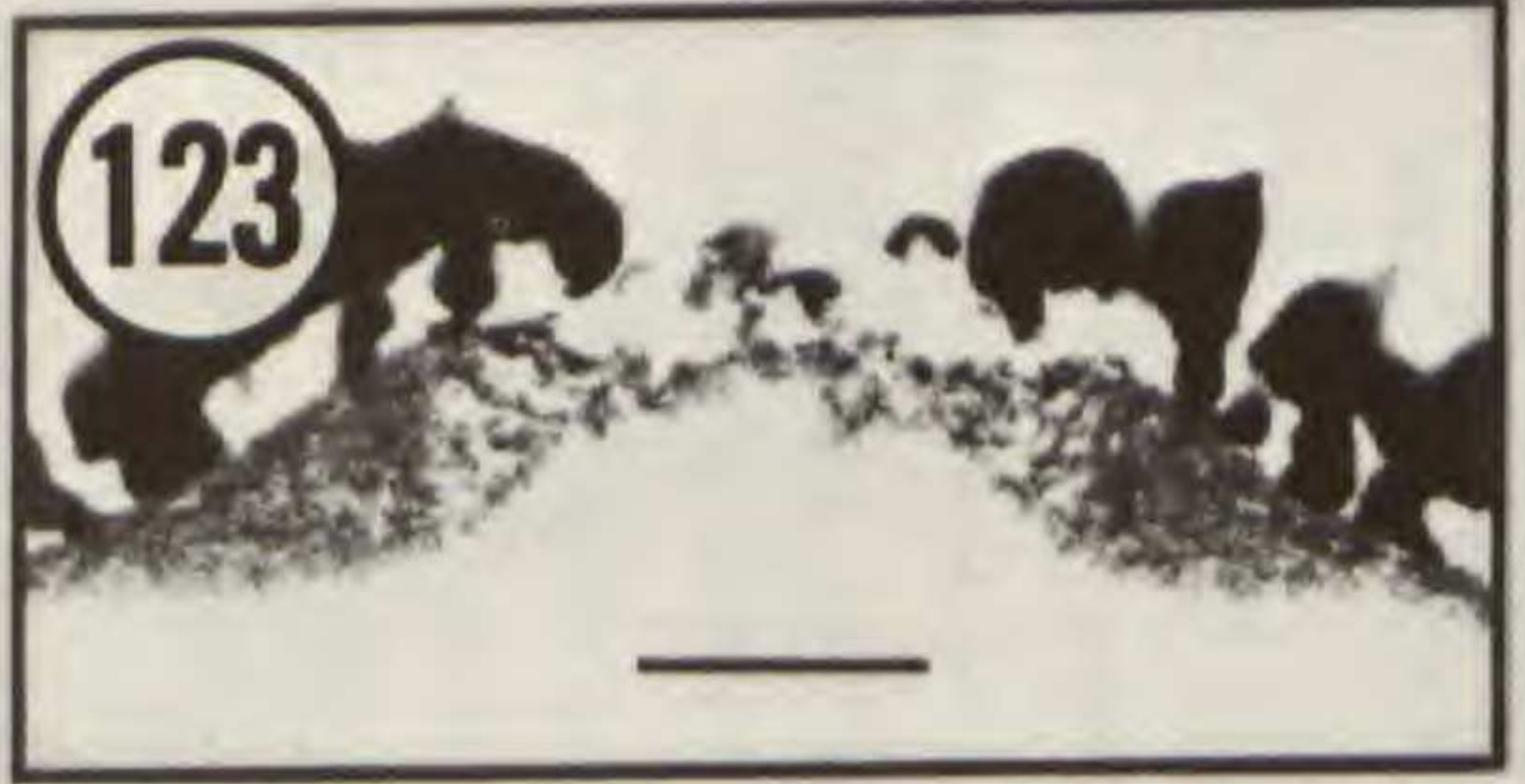
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*Anemone coronaria*, Fig. 149; *Ranunculus muricatus*, Fig. 150; *Coptis occidentalis*, Fig. 151; *Clematis orientalis*, Fig. 152; *Adonis pyrenaica*, Fig. 153; *Eranthis hyemalis*, Fig. 154. In numerous examples Ranunculaceae pollen was indistinguishable from various representatives of centrospermae families, particularly Amaranthaceae, Caryophyllaceae, and Chenopodiaceae. The range of variation in the size and distribution of spines and perforations in the Ranunculaceae was no greater than in some centrospermae families, e.g., Portulacaceae (Nowicke, 1975: figs. 16–17) or Nyctaginaceae (Nowicke, 1975: figs. 8, 12).

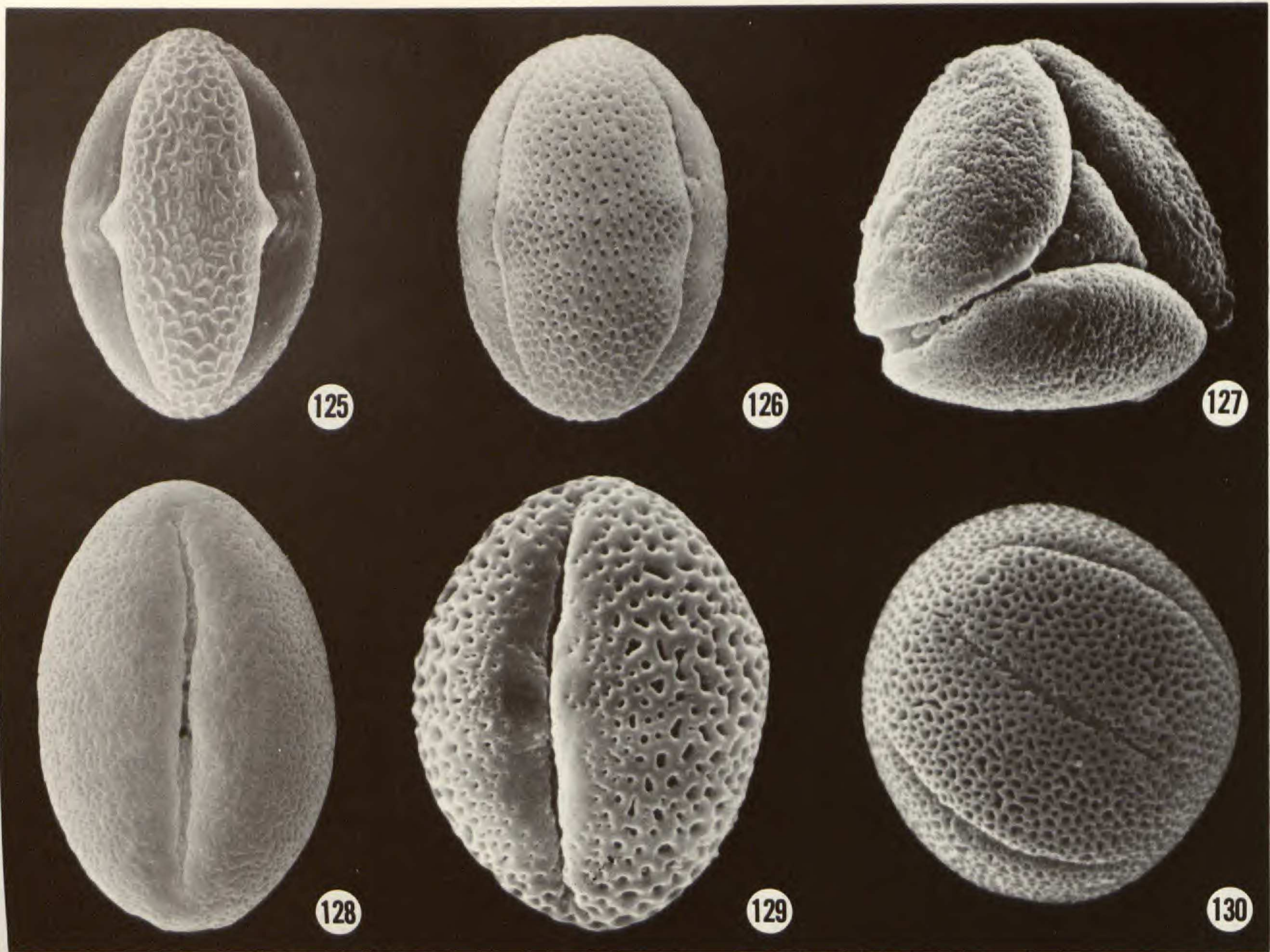
Thus far all taxa examined in the Ranunculaceae have simple apertures (*Paeonia* may be an exception): 3-colpate, e.g., *Clematis orientalis*, Fig. 152, *Adonis pyrenaica*, Fig. 153, and *Eranthis hyemalis*, Fig. 154; pantoporate, e.g., *Anemone coronaria*, Fig. 149, *Coptis occidentalis*, Fig. 151; pantocolpate, *Ranunculus muricatus*, Fig. 150. Other types not illustrated include: 5–8-zonocolpate, 6-pantocolpate, spiral, and irregular. The apertures are frequently variable within a sample, especially in the 3-colpate and 6-pantocolpate types. These grains do not appear sterile, i.e., their size and wall thickness is about the same as in grains with a more precise configuration of the apertures.

The close similarity depicted in SEM between the tectum of the Centrospermae and that of the Ranunculaceae is not paralleled in the structure of the exine. This is not to say that all taxa examined in the Ranunculaceae can be easily distinguished in thin section from the Centrospermae, but rather that some Ranunculaceae have modifications or developments not found in the pollen of the Centrospermae. One of the most consistent differences is the presence of an appreciable endexine in nonapertural regions, as well as beneath the apertures: in *Anemone coronaria*, Fig. 155, the endexine is massive and much thicker than either the foot layer or the tectum; in *Coptis occidentalis*, Fig. 159, the endexine is no doubt enhanced by the slightly oblique angle of section, but it would be prominent even in a perfectly radial section; *Clematis orientalis*, Fig. 156, *Ranunculus muricatus*, Fig. 157, and *Adonis pyrenaica*, Fig. 158, have a readily identified endexine layer. In most of the centrospermae taxa the endexine is usually present only in the region of the apertures.

Many taxa in the Ranunculaceae have modified columellae: larger in size and more sparsely distributed, or, very reduced and the tectum and foot layer scarcely separated. Grains of either type do have a distinctive exine structure. The former modification is illustrated here by *Anemone coronaria*, Fig. 155; it also occurs in species of: *Batrachium*, *Coptis*, *Hamadryas*, *Hepatica*, *Oreithales*, *Ranunculus*, and *Xanthorrhiza*. In the latter condition the columellae in *Adonis pyrenaica*, Fig. 158, and in *Glaucidium palmatum* (unpublished data), are reduced and are not the dominant component in cross-section. *Aconitum* (unpublished data) probably represents the extreme in columellae reduction and in *A. japonicum* only a thin broken line separates the tectum and the foot layer.

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FIGURES 120–124. Transmission Electron Micrographs of Polygonaceae pollen.—120. *Chorizanthe paniculata* Benth.,  $\times 22,680$ .—121. *Podopterus mexicanus* H. & B.,  $\times 12,190$ .—122. *Emex australis* Steinheil,  $\times 4,100$ .—123. *E. australis*,  $\times 9,430$ .—124. *Ruprechtia pallida* Standl.,  $\times 8,510$ .



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None of the Centrospermae examined in thin section have the extremes of columellae development which are found in the Ranunculaceae. Nevertheless, there are certain taxa in the Ranunculaceae which are indistinguishable in thin section from certain taxa in the Centrospermae.

Again, it is a peculiar distribution, an all or none phenomenon, which transforms a seemingly simple tectum into a significant characteristic: the Ranunculaceae is the first noncentrospermous family to have the spinulose and punctate/perforate tectum, and its presence in 111 of the 134 species examined argues compellingly that this family is the closest extant relative of the Centrospermae. Admittedly, neither the betalains nor the protein type sieve-tube plastid have been found in the Ranunculaceae, but it is the very restriction of these two features to the Centrospermae that makes the order unique. To make either or both a prerequisite for relationship to this unusual group of families defeats any investigation before it has begun.

#### BERBERIDACEAE

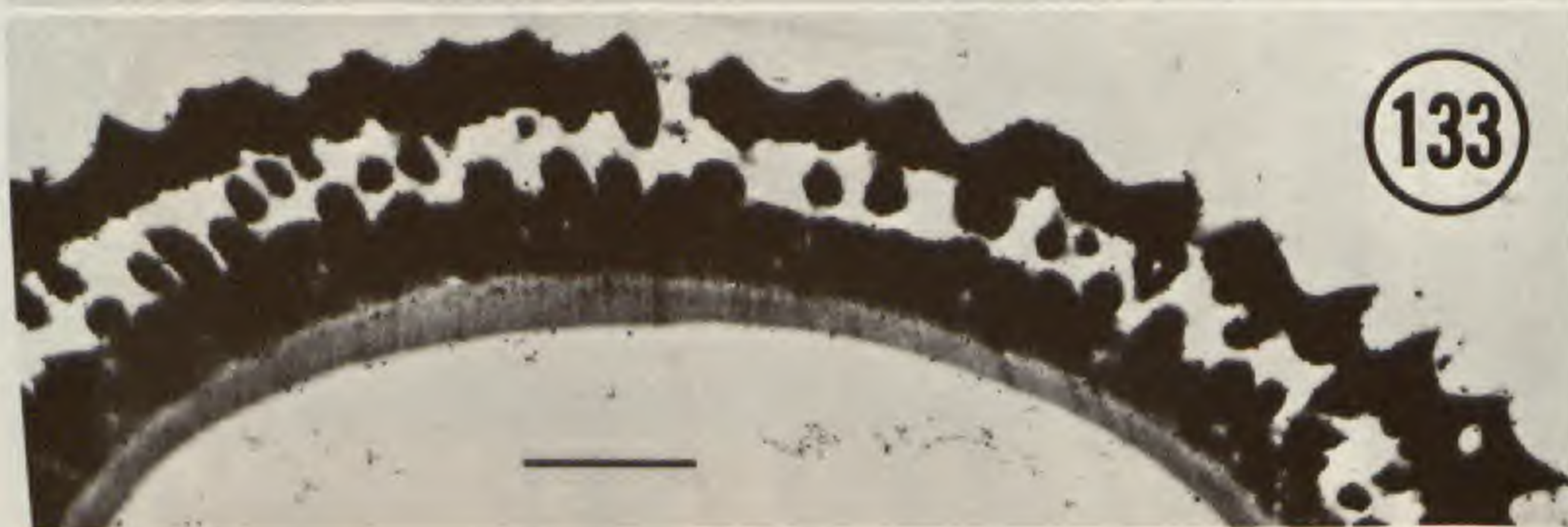
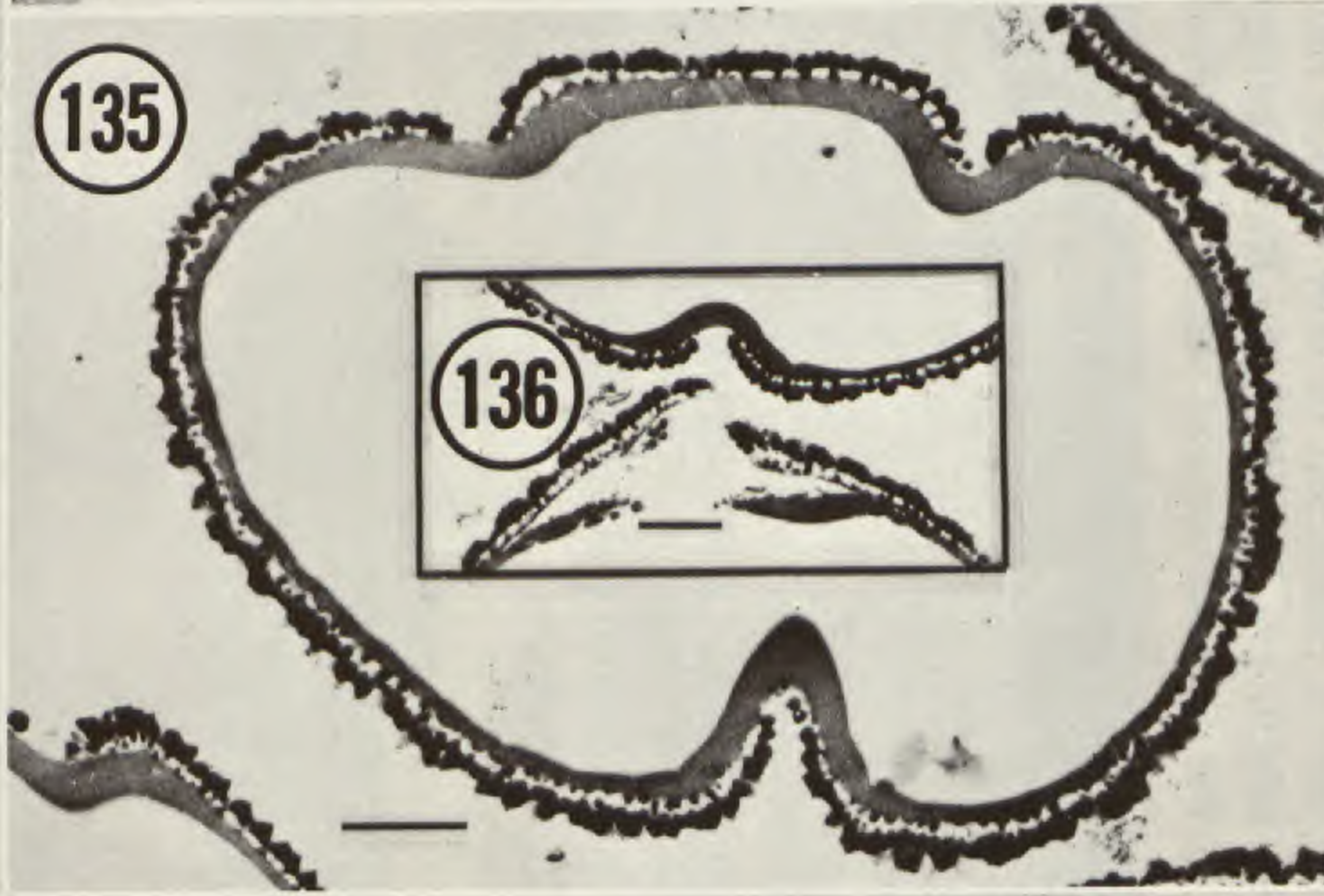
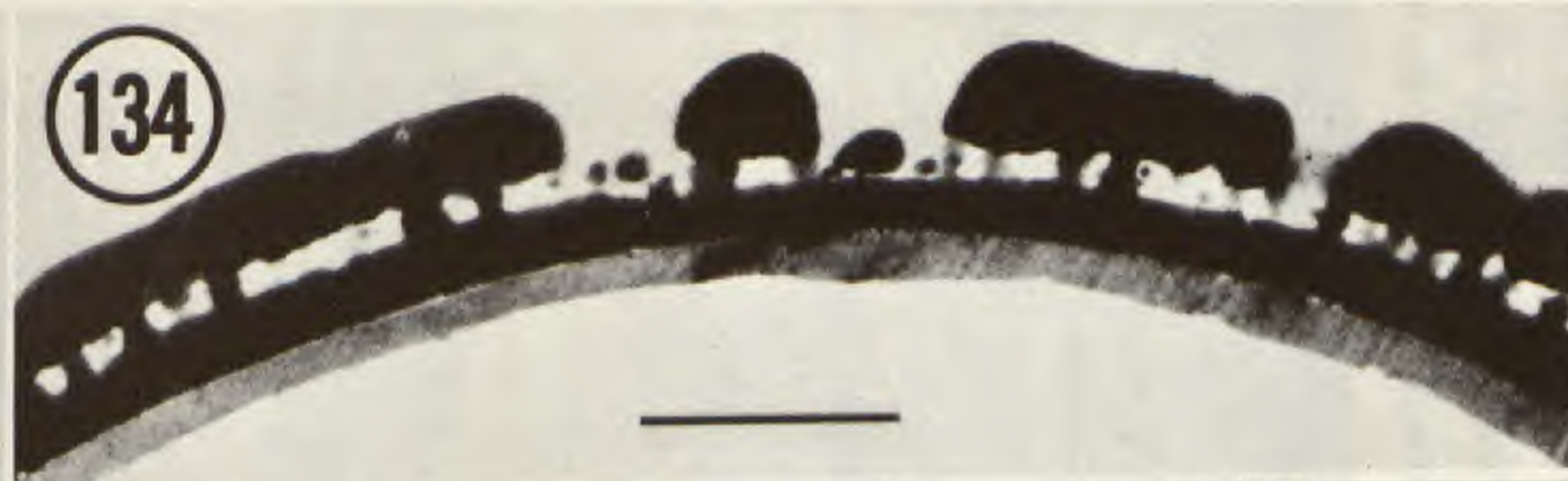
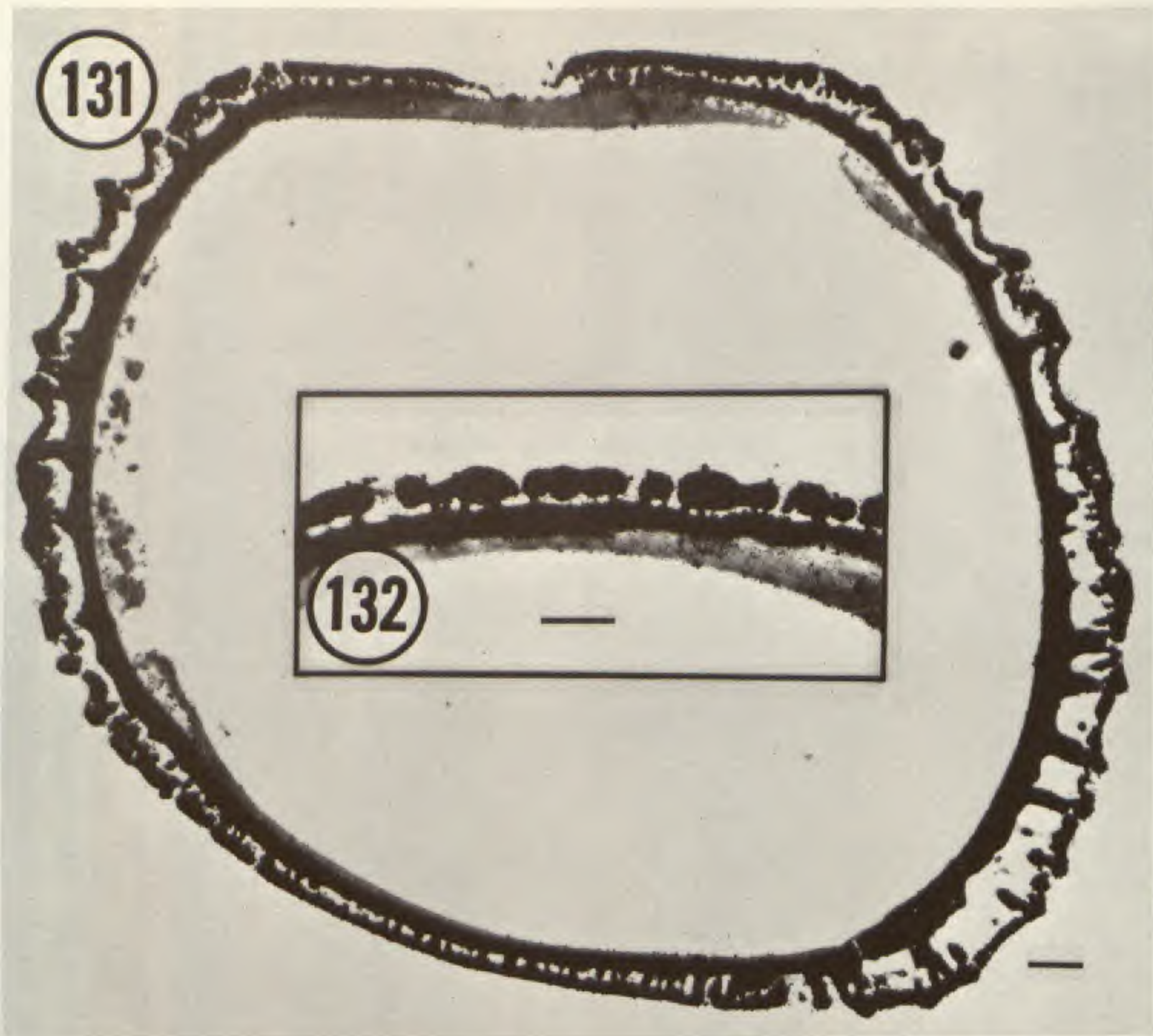
The traditional view of the Berberidaceae s.l. as a group of genera that are not closely related to each other is, in part, clarified and refined by the palynological data (Nowicke & Skvarla, 1979).

*Berberis* L. and *Mahonia* Nutt., illustrated by *B. fendleri*, Figs. 138, 144, and *M. nervosa*, Figs. 141, 145, have almost identical pollen, and this agrees with the close relationship or even congeneric treatment accorded the two genera on other bases. Of far greater significance than the expected similarity is the primitive state of the distinguishing characteristics: irregular apertures consisting of cracks or breaks, or spiral apertures in which the configuration of the furrows is not uniform even within a sample; the exine has an unspecialized or random surface, and psilate, punctate, punctate-striate, and granular can occur within a sample, and sometimes more than one on a single grain; in thin section, Figs. 144–145, the exine is amorphous and only the presence of irregular cavities indicates an early stage of stratification. This type of aperture, exine surface, and wall structure are uncompromisingly primitive and serve to isolate *Berberis* and *Mahonia* from all remaining ones. The woody habit, carpel structure, and chromosome number further distinguish these two genera, and we would agree with Hutchinson's (1959) restricted concept of the Berberidaceae as composed of only *Berberis* and *Mahonia*.

A sufficient pollen sample of *Ranzania japonica* (T. Ito) T. Ito, a relict species confined to the northern end of Honshu, was not obtained until March 1979. Briefly described, the grains are spherical, 6-pantocolpate, the surface unspecialized, and the exine unstratified in thin section.

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FIGURES 125–130. Scanning Electron Micrographs of Primulaceae pollen.—125. *Coris monspeliensis* L., equatorial view,  $\times 1,800$ .—126. *Anagallis linifolia* L., equatorial view,  $\times 2,925$ .—127. *Cortusa matthioli* L., oblique polar view with triangular apocolpial field,  $\times 4,330$ .—128. *Glaux maritima* L., equatorial view,  $\times 2,780$ .—129. *Naumbergia thyrsiflora* (L.) Reichenbach, equatorial view,  $\times 3,680$ .—130. *Primula officinalis* (L.) Jacq., equatorial view,  $\times 4,880$ .



None of the major United States herbaria had material of *Ranzania*, and specimens consisting of the only two collections at Kew were sent to the U.S. National Herbarium in April 1979. Although Terabayashi (1977, 1978) considers the floral morphology of *Ranzania* to be similar to that of *Berberis* and *Mahonia*, and all three have an unstratified exine, the great disparity in vegetative characteristics suggests that the ancestral stock of *Ranzania* separated very early from that of *Berberis-Mahonia*, and that the floral morphology of all three has remained unchanged. (For greater detail and photographs of the *Ranzania* herbarium specimens the reader is advised to consult Nowicke & Skvarla, 1979.)

*Bongardia* C.A. Meyer, *Caulophyllum* Michx., and *Leontice* L. are more closely related to each other than to any other berberidaceous genera in terms of pollen morphology. However, the unifying characteristics, grains which are larger and have a reticulate tectum, are scarcely the type to reinforce the separate family status accorded these genera by Airy Shaw (1966).

*Nandina domestica* Thunb. has been treated as a monotypic family by a number of workers, Takhtajan (1969), Airy Shaw (1966), and Kumazawa (1938). The pollen morphology is not particularly specialized, but the uniformly punctate tectum and a massive endexine distinguish this species from all other taxa in the Berberidaceae s.l. Thus the pollen lends support to those who favor separation of this genus on other characteristics.

The pollen morphology of the disjunct genus *Diphylleia* Michx., represented here by *D. sinensis*, Figs. 140, 148, is unique within the Berberidaceae, and within all of the order Ranunculales examined to date, but of itself has little systematic value. This same statement would apply to the pollen of *Podophyllum emodi*, tetrads that have a tectum of ripple-surfaced gemmae, which have, to our knowledge, no known counterpart in the dicots.

We are aware that in the genus *Podophyllum* L. the difference in pollen morphology between *P. emodi* and *P. peltatum* could be interpreted to be as great or greater than in the family as a whole.

For the remaining genera traditionally placed in the Berberidaceae the pollen data have strong implications regarding their relationships to each other, but admittedly not as definitive as in the case of *Berberis* and *Mahonia*.

The Old World genus *Epimedium*, with perhaps 25 species, has sufficient variation in the tectum to link the New World genus *Vancouveria*, both the Asian and American species of two disjunct genera, *Achlys* and *Jeffersonia*, illustrated by *J. diphylla*, Figs. 142, 147, *Dysosma pleianthum*, and *Podophyllum peltatum*, Figs. 139, 146. The primary or basic tectum consists of randomly distributed small rods with one end free and projecting slightly outward. The tectum in most of the above taxa has been modified principally by the loss of some of the distinction of the individual rods. In four species of *Epimedium*, *E. cremeum*, *E.*

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FIGURES 131–137. Transmission Electron Micrographs of Primulaceae pollen.—131. *Coris monspeliensis* L.,  $\times 5,040$ .—132. *Glaux maritima* L.,  $\times 6,840$ .—133. *Anagallis linifolia* L.,  $\times 11,040$ .—134. *Naumbergia thyrsiflora* (L.) Reichenbach,  $\times 14,210$ .—135. *Cortusa matthioli* L.,  $\times 8,100$ .—136. *C. matthioli*,  $\times 6,090$ .—137. *Primula officinalis* (L.) Jacq.,  $\times 41,650$ .



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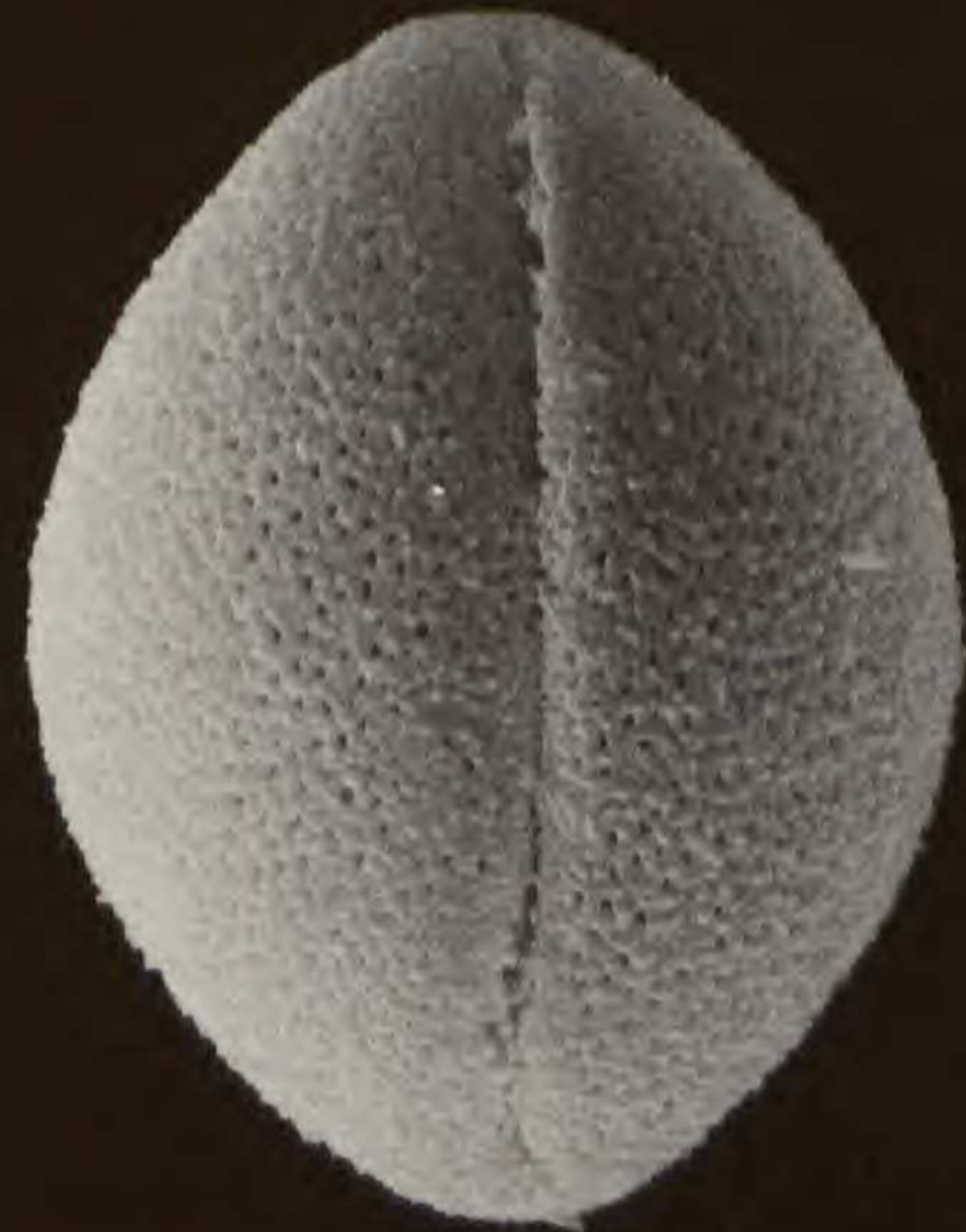
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*diphylla*, *E. grandiflora*, and *E. sempervirens*, Fig. 143, and most collections of *P. peltatum*, there are grains in which the rods are still discernible. And, there are some grains in all four taxa in which five, six, or seven of the tips are arranged like the vanes of a pinwheel. The range of variation within each sample is such that an almost perfect continuum exists among the above four species (Nowicke & Skvarla, 1979).

The type of pollen morphology found in *Hydrastis* L. indicates that the genus is more closely related to the tribe Epimedieae than to any taxa in the Ranunculaceae. *Hydrastis* is one of the four genera in the Ranunculaceae which does not have a spinulose and punctate/perforate tectum, and the only one with a striate-reticulate tectum very similar to some species in *Epimedium* and *Vancouveria*. Dahlgren (1975) and Takhtajan (1969) treat *Hydrastis* as a monotypic family, while Airy Shaw (1966) includes the monotypic genus *Glaucidium* as well, citing features which link these two species to the Ranunculaceae on one hand and to the Berberidaceae on the other. But considering the distribution of the striate-reticulate tectum in the Ranunculales, we would place *Hydrastis* in the alliance of *Epimedium*, *Vancouveria*, *Jeffersonia*, and *Achlys*.

*Glaucidium palmatum*, which has been segregated with *Hydrastis* as either a family or subfamily in the Ranunculaceae, has 3-colpate grains with a punctate/spinulose tectum in which the punctae are sparsely distributed and the spinules are more numerous, and uniform in size and distribution. In both SEM and in TEM (unpublished data), the pollen is very similar to that of *Adonis pyrenaica*, Figs. 153 and 158. The pollen morphology does not indicate a close relationship with *Hydrastis*, nor would it reinforce the monotypic separate family status accorded by Dahlgren (1975) and Takhtajan (1969).

#### CORYNOCARPACEAE AND CORIARIACEAE

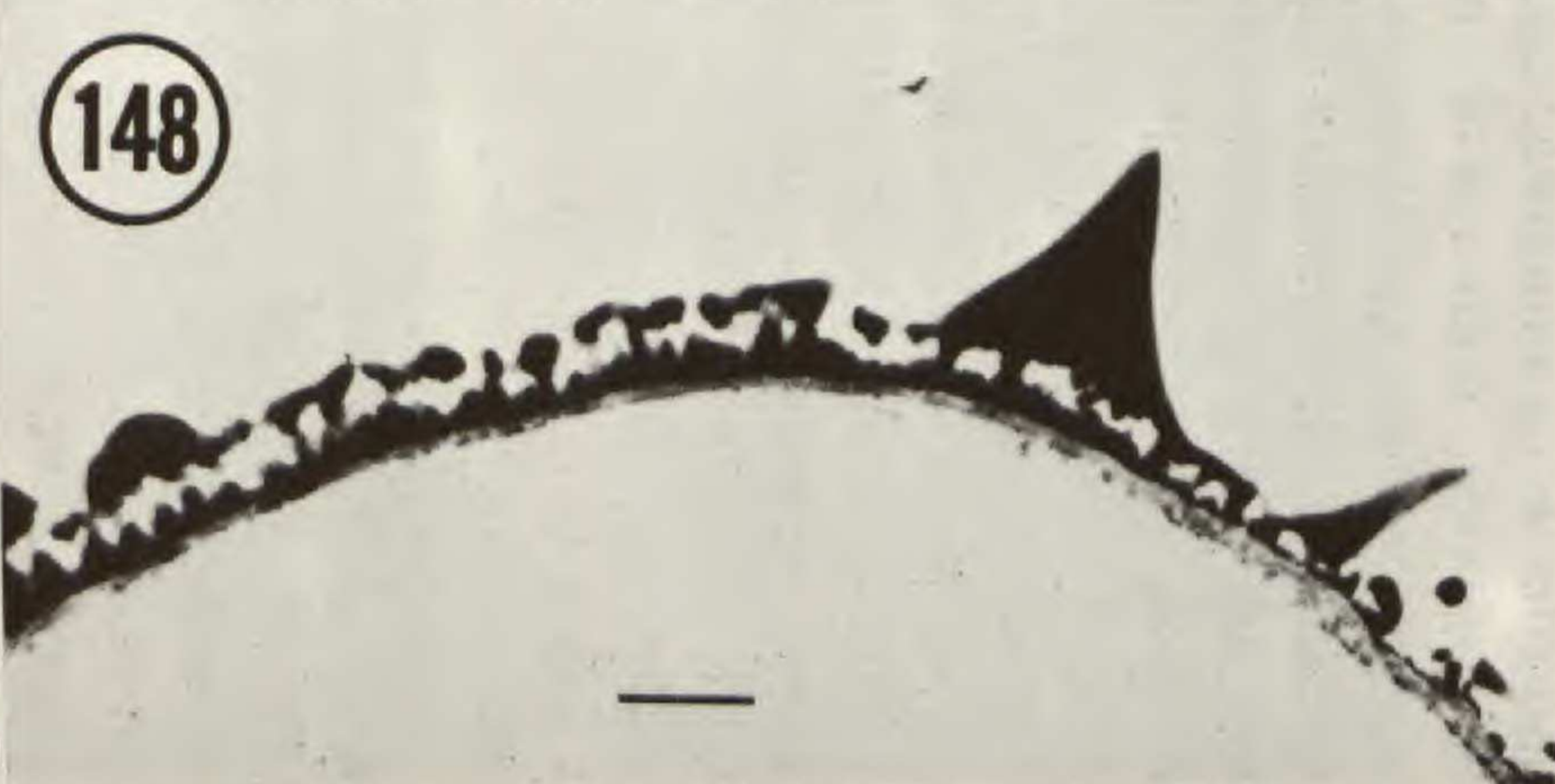
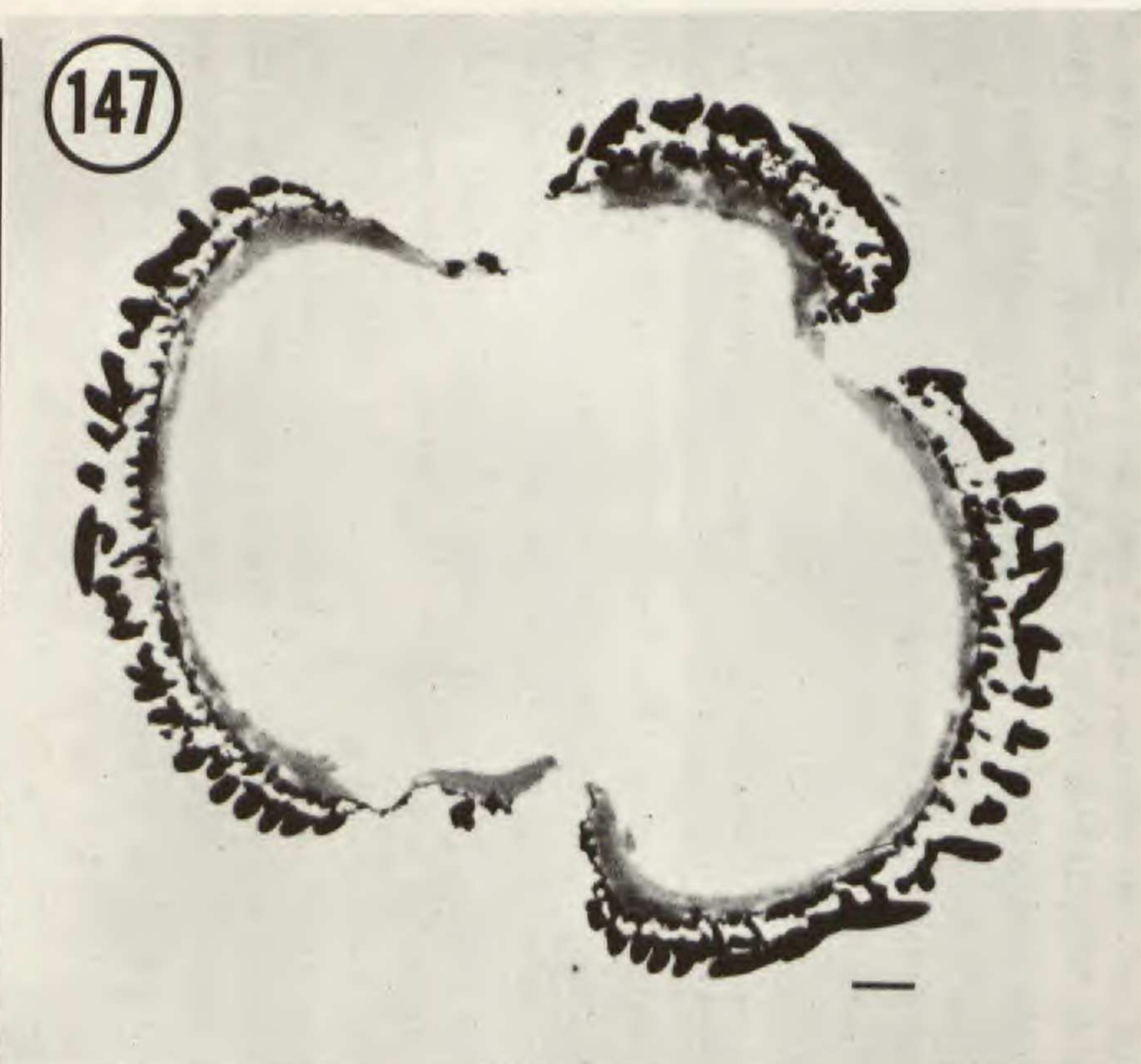
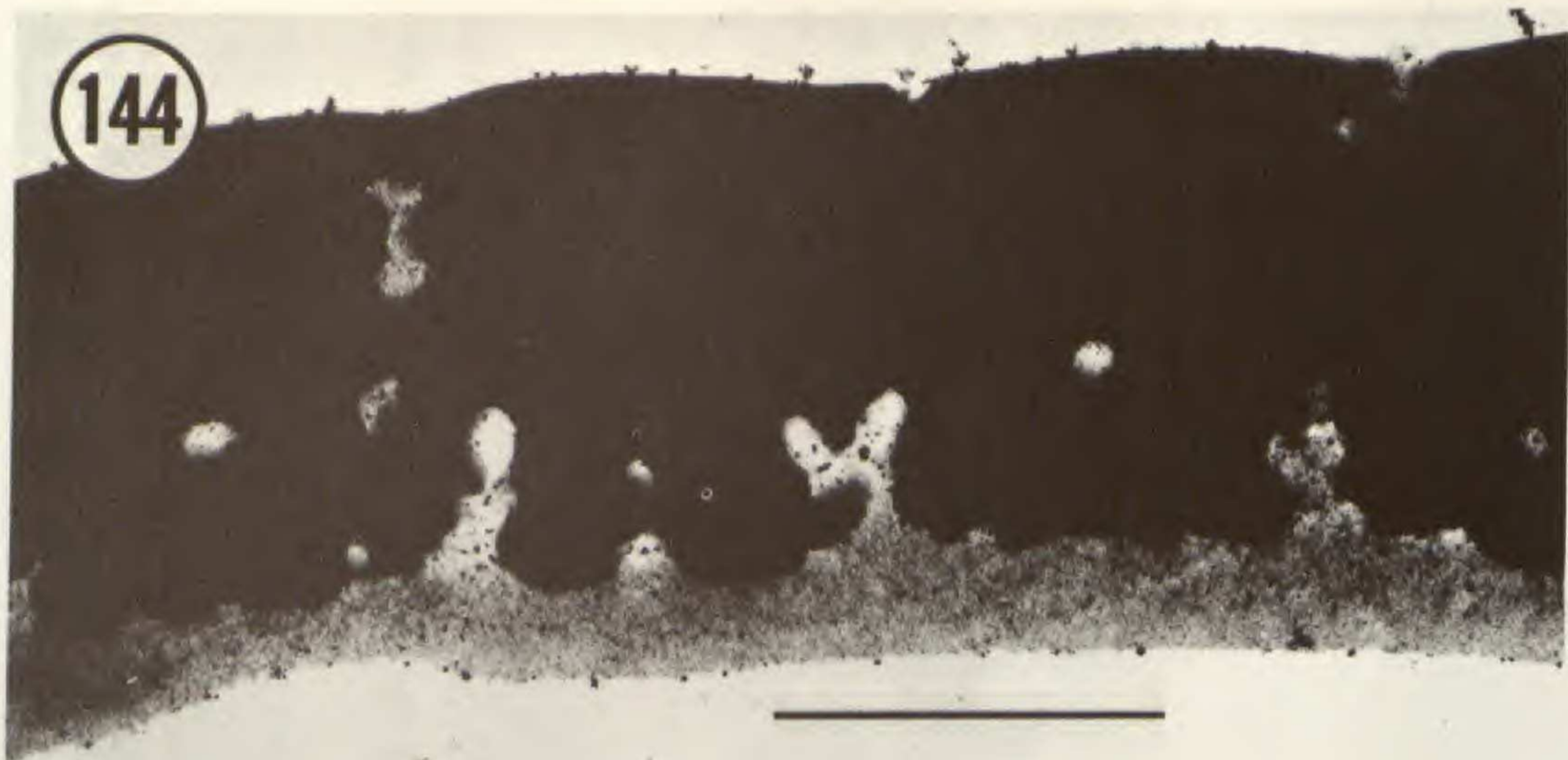
The following reports on the pollen morphology of the Corynocarpaceae and Coriariaceae are based on a very limited sample and should be considered with reserve, although our preliminary results do agree with those of Erdtman (1966).

The Corynocarpaceae, consisting of a single genus with five species distributed in the southwest Pacific (Australia, New Zealand, New Caledonia, etc.), is only doubtfully referred to the Ranunculales by Cronquist (1968). The pollen of the one species available to this study, *Corynocarpus laevigata*, is sufficiently distinct to make it a key characteristic for the family's placement: the grains have a bilateral symmetry; the shape is extremely oblate in equatorial view; the apertures consist of two short, horizontal and opposite colpi; the surface is more or less psilate; in thin section the exine is relatively undifferentiated. Thorne (1976) placed the Corynocarpaceae in the order Rosales, suborder Cunoniinea,

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FIGURES 138–143. Scanning Electron Micrographs of Berberidaceae pollen.—138. *Berberis fendleri* A. Gray,  $\times 1,420$ .—139. *Podophyllum peltatum* L., slightly oblique polar view,  $\times 2,120$ .—140. *Diphylleia sinensis* Li, polar view,  $\times 1,690$ .—141. *Mahonia nervosa* (Pursh) Nutt.,  $\times 980$ .—142. *Jeffersonia diphylla* (L.) Pers., slightly oblique polar view,  $\times 2,460$ .—143. *Epimedium sempervirens* Nakai, equatorial view,  $\times 2,125$ .





and adjacent to the Staphyleaceae. At this time, any comments about the relationships and affinities of Corynocarpaceae would be speculative.

The pollen morphology found in the Coriariaceae does little to clarify its systematic relationships except, perhaps, to interpret the distinction from all other taxa examined as evidence that it does not belong in the order Ranunculales. The close agreement of the pollen in the four species examined, *Coriaria japonica* A. Gray, *C. myrtifolia* L., *C. ruscifolia* L. and *C. thymifolia* Willd. would remove any doubt about their natural relationship: the grains are suboblate, spheroidal, sometimes angulaperturate in shape; the apertures are 3(–4) pores or very short colpi, sometimes with a thickened margin, placed on the presumed equator; the tectum coarsely granular. The only species examined in thin section, *C. ruscifolia*, has typical dicot stratification: a thin but consistent endexine, diminutive columellae connecting an uneven but probably continuous tectum with a thin, uniform foot layer. It is this unit which is thickened abruptly near the apertures that produces the external crassi-marginate characteristic. It is impossible to deal adequately with families such as this or Corynocarpaceae in a review paper except negatively, i.e., the pollen morphology does not support the present placement of the family in the order Ranunculales. Thorne (1976) has placed the Coriariaceae next to the Simarubaceae and Rutaceae, both of which are known to have a diversity of pollen types. Whether the range of variation would include the one described above remains unanswered.

[Additional pollen samples have been obtained, but not yet examined, for both families. We intend to explore the relationships of the Corynocarpaceae and of the Coriariaceae as suggested by Thorne (1976), and will treat each family in a separate publication.]

#### LARDIZABALACEAE

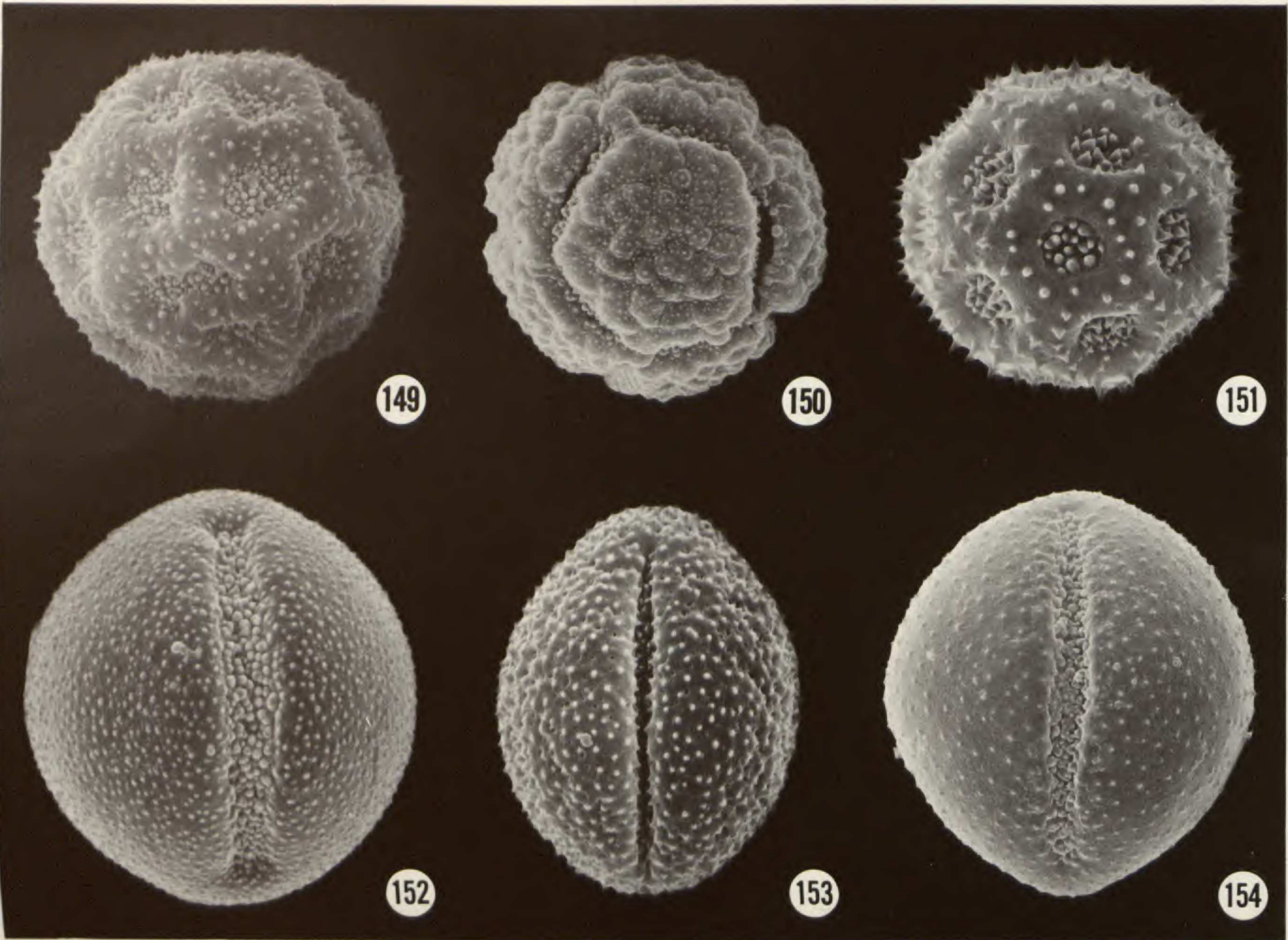
The Lardizabalaceae have an unusual distribution, southeast Asia from Nepal to Japan, and Chile. The pollen of 14 species representing 7 genera was examined: *Akebia*, *Boquila*, *Decaisnea*, *Holboellia*, *Lardizabala*, *Parvatia*, and *Stauntonia*. With the possible exception of *Stauntonia hexaphylla*, all taxa had 3-colpate aperture types. In *Akebia*, *Boquila*, and *Holboellia* the colpi are wide and do not taper at the poles. In most taxa the tectum is complete except for punctae of varying size and distribution. A general similarity also exists in thin section: a well-developed endexine, thin foot layer, diminutive, uniform columellae, and a tectum that is the most conspicuous of the ectexine units.

#### DILLENACEAE

The investigation of the Dilleniaceae was prompted by the transfer of *Paeonia* from the Ranunculaceae to the order Dilleniales and its elevation to family status,

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FIGURES 144–148. Transmission Electron Micrographs of Berberidaceae pollen.—144. *Berberis fendleri* A. Gray,  $\times 25,350$ .—145. *Mahonia nervosa* (Pursh) Nutt.,  $\times 11,310$ .—146. *Podophyllum peltatum* L.,  $\times 12,880$ .—147. *Jeffersonia diphylla* (L.) Pers.,  $\times 4,200$ .—148. *Diphylleia sinensis* Li,  $\times 7,380$ .



Paeoniaceae. The pollen of approximately 40 species was examined in LM and in SEM, and the following comments are based on this restricted number and technique. Variation within a species and within a sample suggests that pollen morphology will have limited value. There are some species of *Curatella*, of *Davilla* and of *Doliocarpus* that have pollen similar to some species of *Paeonia*: grains which are prolate, 3-colporate (colporoidate), and an incomplete tectum in which the perforations are smaller nearer to the colpi. This type of morphology is a common one in the dicots, and illustrated in this paper by Fig. 129, *Naumburgia thyrsiflora* (Primulaceae) and in *Lysimachia terrestris* (Nowicke & Skvarla, 1977: fig. 177). Some species of *Paeonia* have a pollen morphology similar to that of *Lysimachia hybrida* (Nowicke & Skvarla, 1977: fig. 175) including the bridge of ectexine across the colpus. The type of tectum in *Paeonia brownii*, Fig. 160, in which the perforations are more uniform in size, was not found in the taxa examined of Dilleniaceae. *Actinidia* and allied genera, *Clematoclethra* and *Saurauia*, sometimes recognized as a separate family, Actinidiaceae, are more closely related to each other than to any remaining members of Dilleniaceae. This distinction, a continuous or complete tectum, is not very great, and if additional species of Dilleniaceae s.l. are examined, it may well be lost.

The Dilleniaceae pollen will be examined in thin section and information from exine structure may clarify some of the above relationships.

#### ADAPTIVE SIGNIFICANCE

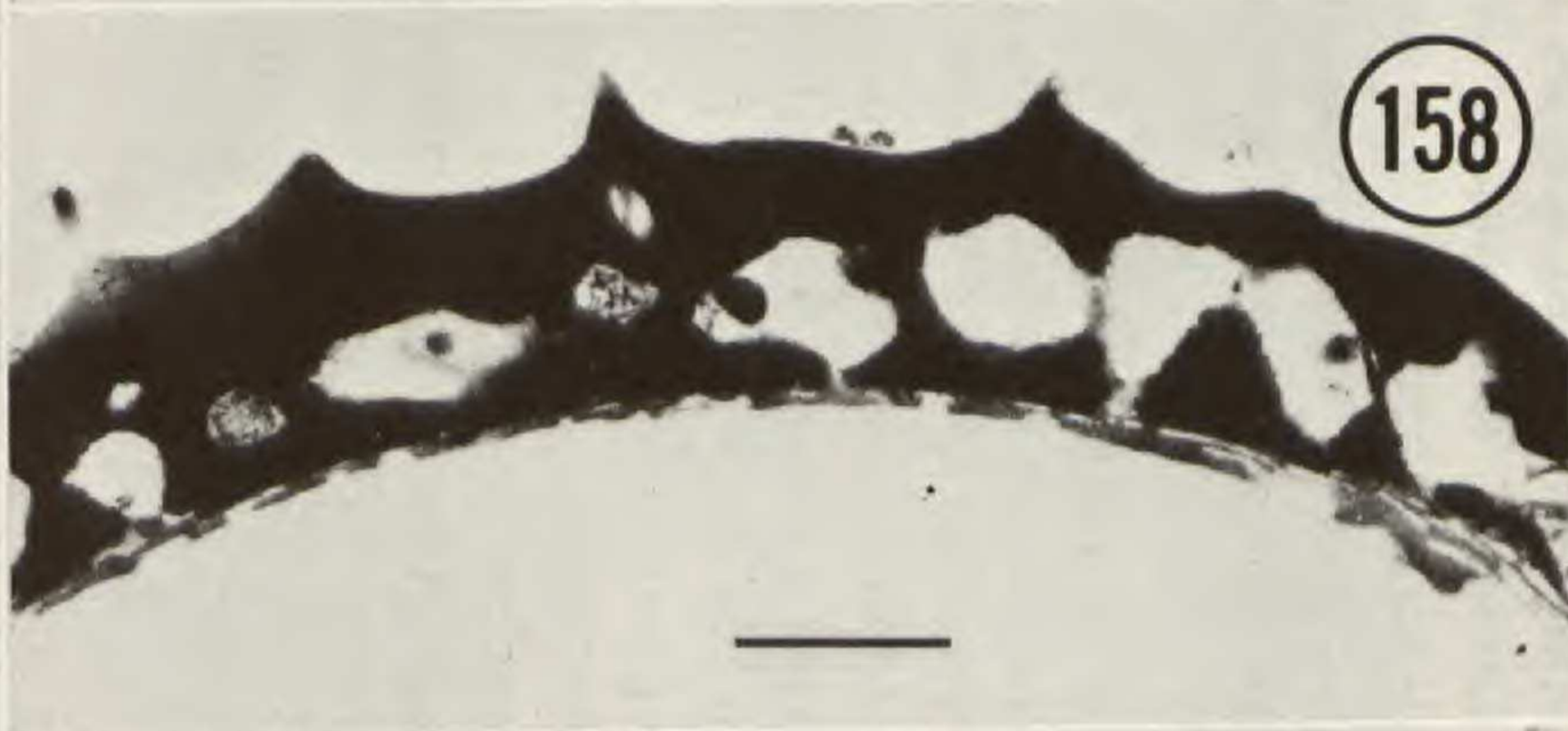
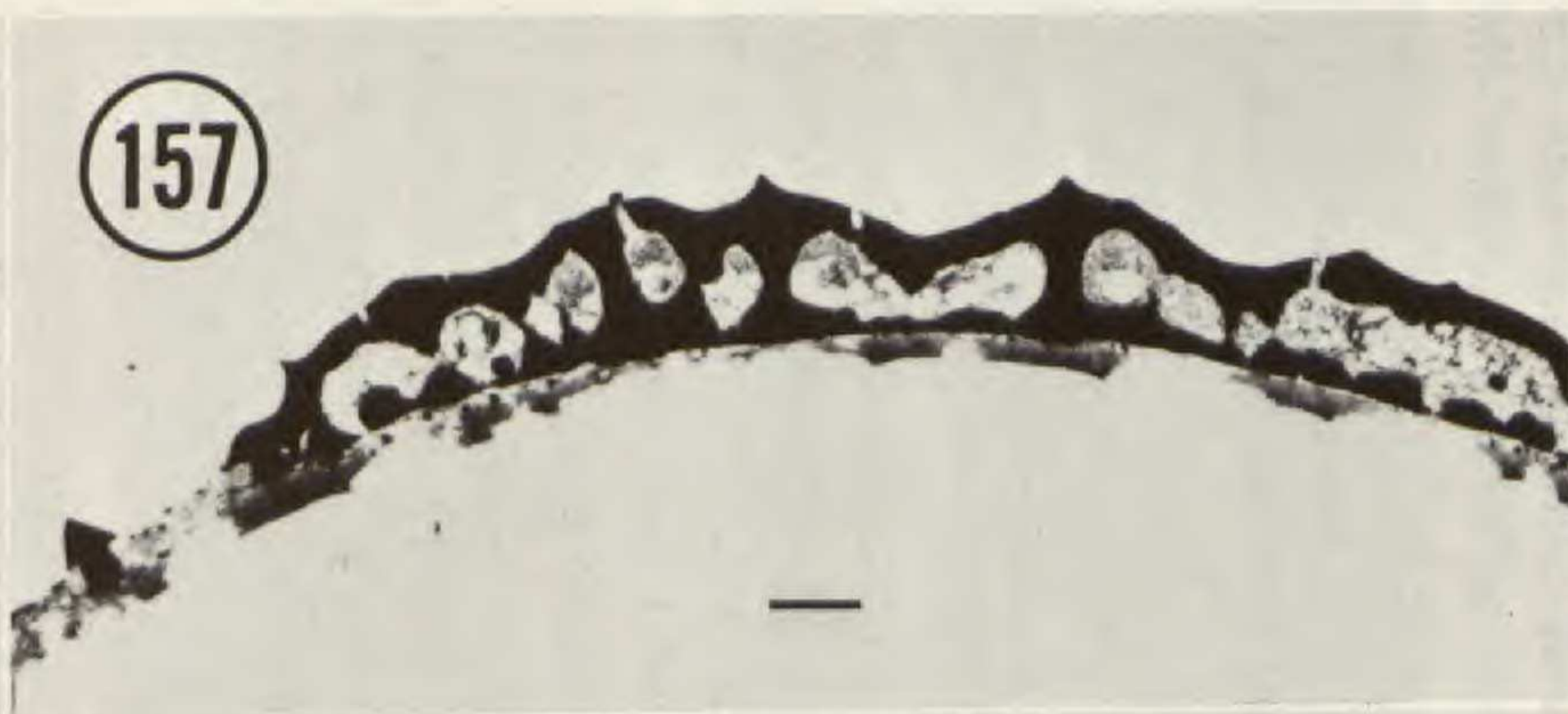
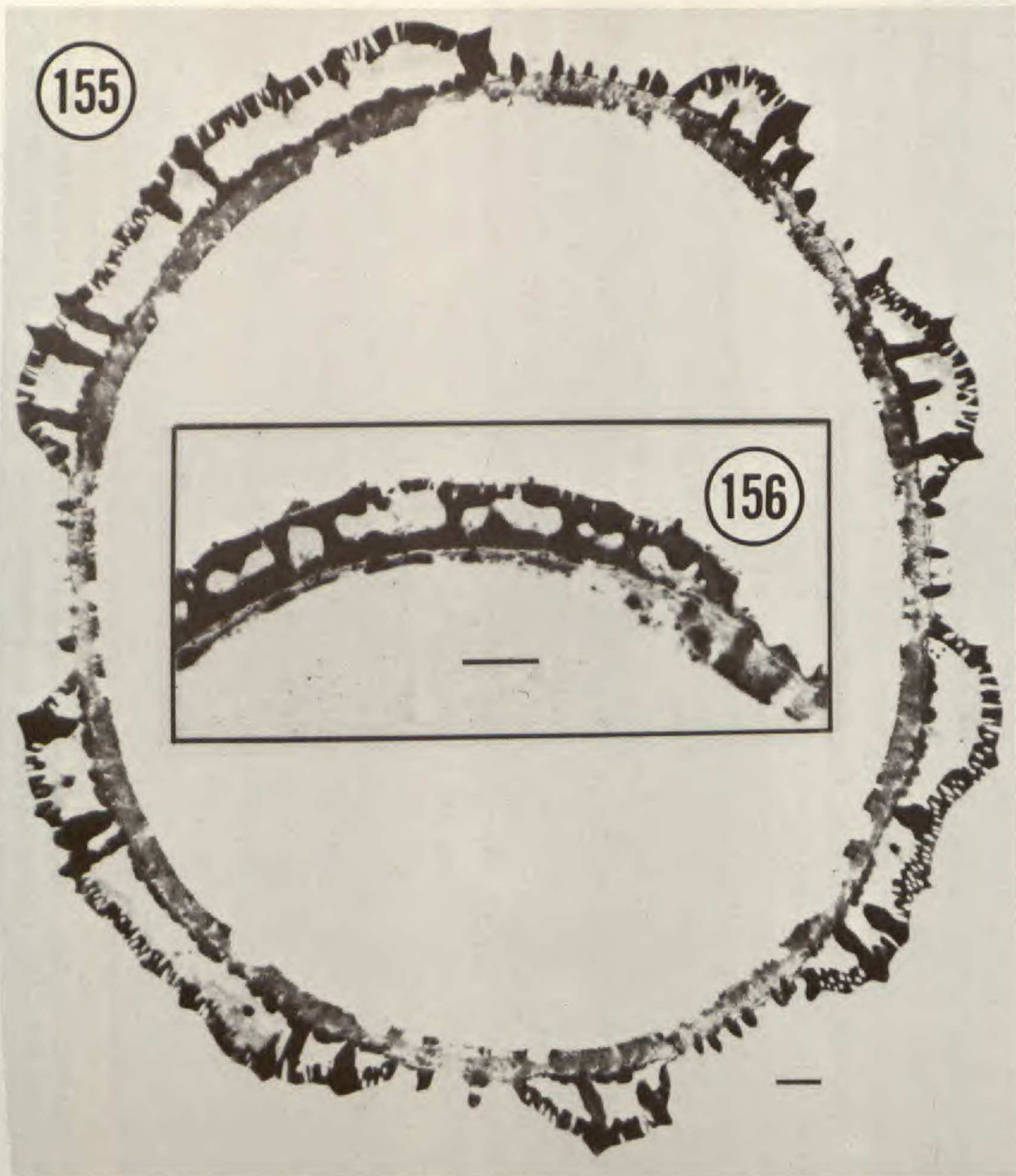
In a review article which spans such a large number of taxa, the great range of variation in the surface of the tectum, and to a lesser extent in the aperture types and exine structures, raises the fundamental question of the adaptive significance of the variation. There are some correlations between the function of the pollen grain, which is to transfer the male gametophyte and to insure germination, and certain characteristics of the exine.

Protection from desiccation during transfer is basic and the architecture of the wall could logically be interpreted as an adaptation to minimize the effects of water loss: the two concentric spheres (or other shapes), i.e., the foot layer and tectum, whose spatial separation is maintained by the columellae, provides maximum support and rigidity. Adaptations for germination are more conspicuous: preformed breaks in the exine expedite the release of the nuclei; more than one potential exit would permit rapid germination no matter what area of the grain might be in contact with the stigma. A function has been attached to the chamber between the foot layer and tectum: storage of recognition substances that initiate the process of germination. The apertures also function as harmomegathic mechanisms (Wodehouse, 1935; Payne, 1972).

The great diversity in the surface of the tectum is another matter altogether. In Heslop-Harrison's view (1971: 8): "Evidently if we are not to assume that pollen wall sculpturings are no more than meaningless manifestations of a kind

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FIGURES 149–154. Scanning Electron Micrographs of Ranunculaceae pollen.—149. *Anemone coronaria* L.,  $\times 1,780$ .—150. *Ranunculus muricatus* L.,  $\times 1,240$ .—151. *Coptis occidentalis* (Nutt.) T. & G.,  $\times 2,270$ .—152. *Clematis orientalis* L., equatorial view,  $\times 2,530$ .—153. *Adonis pyrenaica* DC., equatorial view,  $\times 1,780$ .—154. *Eranthis hyemalis* (L.) Salisb., equatorial view,  $\times 1,560$ .



of morphogenetic virtuosity, we must accept that there is a high adaptive component, and that diversity has resulted from selective forces." But has all of the diversity been the result of selective forces?

Of all possible structure-function correlations in pollen morphology, that of pollen-pollination vector has probably attracted the most attention and produced the least consistent results.

Leuenberger (1976: 203), after examination of 600 species in the Cactaceae, reported that "The data obtained so far do not support the assumption that clear correlations exist between exine sculpturing and pollination types."

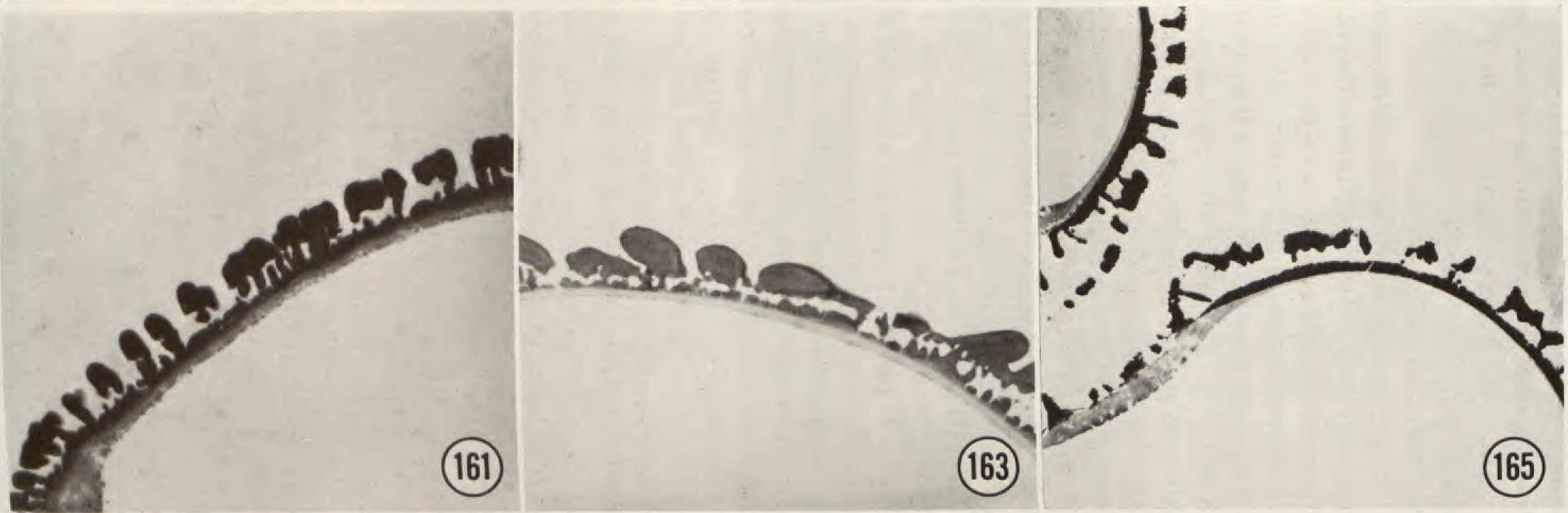
Taylor & Levin (1975) reported similar and wider conclusions in the Polemoniaceae. In their discussion they note that (p. 104) "it is appropriate to question at this point whether different exine organization patterns reflect adaptations to different pollen dispersal mechanisms. The data presented here do not substantiate such a relationship." Nor did they find a relationship between pollen ornamentation and environmental parameters. And, while conceding that features of wall configuration might prove to be correlated with some parameters, Taylor and Levin considered the adaptive significance of the various patterns to be a matter of conjecture. (It should be added that none of the Polemoniaceae are known to be wind pollinated.)

However critical may be the need to control desiccation in wind-pollinated grains, the priority appears to be buoyancy. In this transfer method each individual grain has the entire surface exposed to climatic stress. Most animal-pollinated grains have a pollenkitt, an oily-waxy coating that prevents or reduces evaporation from the surface of the grain. The pollenkitt also causes the grains to clump together, and during transfer those grains in the interior of these sticky masses are protected from physical damage as well. Wind-pollinated grains lack, apparently, adaptations which would reduce water loss. The same coating which would reduce evaporation would probably cause the grains to clump with loss of buoyancy; a thicker exine, which might withstand early collapse due to the shrinking volume of protoplasm, would add weight and loss of buoyancy. In fact, even the size of these grains is disadvantageous in preventing desiccation. The volume of a sphere increases with the cube of the radius while the surface increases with the square of the radius; thus smaller grains present more surface area per unit volume than larger spheres. Admittedly in the wind-pollinated Gramineae, characteristics of the aperture, one crassimarginate pore with an aperture plate, could logically be interpreted as adaptations to reduce desiccation.

On the other hand, the predominantly wind-pollinated Amaranthaceae and Chenopodiaceae have grains with numerous small pores, e.g., Fig. 9, fewer but larger pores, e.g., Figs. 28 and 34, or larger and recessed pores, e.g., Figs. 29–30, 35–36. Structural modifications that provide additional support, such as a thick tectum, e.g., Figs. 41–42, and 48, and/or robust columellae, e.g., Fig. 48, may function to counteract the desiccating properties of the apertures, but not without a loss of buoyancy.

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FIGURES 155–159. Transmission Electron Micrographs of Ranunculaceae pollen.—155. *Anemone coronaria* L.,  $\times 4,200$ .—156. *Clematis orientalis* L.,  $\times 7,540$ .—157. *Ranunculus muricatus* L.,  $\times 5,040$ .—158. *Adonis pyrenaica* DC.,  $\times 11,730$ .—159. *Coptis occidentalis* (Nutt.) T. & G.,  $\times 11,020$ .



It may well be that cryptic mechanisms residing in the cytoplasm function to reduce water loss, perhaps in the same manner that permits halophytes to absorb water against the gradient, but this is active absorption and expends energy.

The adaptive significance of the tectum diversity has become more obscure with an increasing number of results or observations which appear contradictory. In particular, there are two somewhat paradoxical phenomena that are difficult to reconcile in a limited framework of structure/function. On the one hand, quite diverse tecta or even pollen morphologies occur within the same genera, while, on the other hand, the same or very similar, specialized tecta and sometimes pollen morphologies occur in unrelated genera of widely separated families.

The first phenomenon is well known and there are numerous examples. Three examples from our own studies can be cited. The large genus *Tournefortia* has four pollen types, one of which, III, is remarkably distinct (Nowicke & Skvarla, 1974). In vegetative and floral morphology *Podophyllum emodi* and *P. peltatum* are obviously closely related, but palynologically they are widely separated (Nowicke & Skvarla, 1979). *Polygonum* s.l. may have the greatest pollen diversity in the angiosperms (Hedberg, 1947; Nowicke & Skvarla, 1977).

The second phenomenon depends upon the demonstration or proof of pollen similarity, and for the most part the discovery of very similar pollen in widely separated families is the direct result of a technological advancement, the scanning electron microscope. The examples may not be as numerous as in the first case, but it is only a matter of time.

The pollen morphology found in *Tournefortia angustifolia* and related species, Type II (Nowicke & Skvarla, 1974: figs. 10–18), is very similar to that of some members of *Sonneratia* (Muller, 1969: plate IV, fig. 5, plate XI, figs. 1–2).

*Phyllanthus casticum* in the Euphorbiaceae (Bor, 1979: plate VIII, fig. 5), admittedly a member of a eurypalynous genus, is nonetheless very similar to *Schisandra grandiflora* in the Schizandraceae (Walker, 1974: fig. 42), and these families are not considered to be related.

*Simmondsia*, a monotypic genus found in the warm arid regions of North America, is one of the dicot taxa of uncertain affinities. The tectum is (almost?) identical (Nowicke & Skvarla, unpublished data) to that found in *Valeriana palmeri* (Clarke, 1978: fig. 12), although the aperture condition, three poorly defined pores, is not.

If palynologists and systematists accept the view that pollen variation has a high adaptive component, then all of the above examples, either the diversity of pollen in closely related species, or the similarity of pollen in widely separated taxa, can be attributed only to selective forces.

Although Taylor & Levin (1975) avoid the use of selective forces, the following quotation from their *Phylogenetic Interpretations* is of considerable interest (pp. 110–111): "Scanning electron microscopy may prove to be a very valuable tool

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FIGURES 160–165. Scanning Electron Micrographs and Transmission Electron Micrographs of Ranunculaceae pollen.—160. *Paeonia brownii* Dougl., SEM, slightly oblique polar view,  $\times 1,990$ .—161. *P. brownii*, TEM,  $\times 6,350$ .—162. *Trollius acaulis* Lindl., SEM, polar view,  $\times 2,370$ .—163. *T. acaulis*, TEM,  $\times 6,350$ .—164. *Helleborus viridis* L., SEM, equatorial view,  $\times 1,920$ .—165. *H. viridis*, TEM,  $\times 1,020$ .

in elucidating species relationships within the Polemoniaceae, especially if pollen morphology is largely free from the confronting elements of parallel evolution. This rule of thumb may be applied to the pollen morphology of the Polemoniaceae, although with due caution. Implicit in our argument is the proposition that congruity in wall architecture is not the product of parallel evolution, but is the manifestation of long-standing structural similarity dictated by common ancestry. We fail to identify any environmental conditions, biotic or abiotic, which may account for parallel evolution. The adaptive radiation in pollen morphology leading to major 'pollen lineages' ostensibly was initiated and nearly completed long ago, in contrast to more recent differentiation within genera for other aspects of their pollination biology."

The lack of success in identifying environmental conditions and/or selective forces, either on the part of Taylor & Levin (1975) or us, does not deny their existence, but data from studies such as those on the Polemoniaceae and the Cactaceae (Leuenberger, 1976) and the discovery of similar pollen in widely separated taxa could be interpreted as evidence that some pollen variation stems from relictual adaptations. The most plausible explanation of the close similarity of specialized pollen morphologies in the Caryophyllaceae and the Amaranthaceae would be common ancestry. But if the adaptive significance of pollen characteristics is obscure in the present, it is unlikely to be clarified in the past.

#### SUMMARY AND CONCLUSIONS

Within the angiosperms there are an estimated 300 families whose segregation into orders is based on the same premise as all the preceding and lower ranks: these particular families (genera, species, etc.) are thought to be more closely related to each other than to any remaining ones. But the distinction between family and order is of much greater magnitude than between genera and families. The characteristics that define orders are frequently so generalized that their presence in a group of families is as likely to indicate parallel or convergent evolution as it is relationship and/or a monophyletic origin. Many of the larger orders are thought to be artificial, and it is not uncommon to find a family "doubtfully referred to . . ." or "largely for convenience . . . ."

The above reservations do not apply to the Centrospermae, and with at least 13 families and 10,000–12,000 species, it is the best example of a large, natural order in the dicotyledons. These families are united by a series of embryological characteristics which would satisfy the most ardent splitter, but two unique variations, one chemical, the betalains, the other cellular, protein sieve-tube plastid, are responsible for the order's great prominence in systematic research of the last decade.

Pollen morphology, more specifically the presence of a spinulose and punctate/perforate tectum in the vast majority of the taxa examined in the Centrospermae (Table 2), reinforces the close relationship accorded these families from other sources (Table 2). We would include these families in the Centrospermae: Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Caryophyllaceae (including *Geocarpon*?), Chenopodiaceae (including *Dysphania*), Didiereaceae, Halophytaceae, Molluginaceae, Nyctaginaceae, Phytolaccaceae (including *Stegnosperma*), and Portulacaceae (including *Hectorella* and *Lyallia*?).



TABLE 2. Summary of results of pollen analysis.

	Taxa Examined	Ektexine	
	Species/Genera	Spin. + Tub./Punct.	"Other" <sup>a</sup>
Plumbaginaceae (10–15)	20/9	0	20
Polygonaceae (40)	100/40	4	96
Primulaceae (28)	29/22	0	29
Betalain Families plus Caryophyllaceae and Molluginaceae	238	205	33
Ranunculaceae	134/42	111	23
Berberidaceae	39/13	0	39
Lardizabalaceae	14/9	0	14
Dilleniaceae	41/13	0	41

<sup>a</sup> Any tectum other than spinulose/punctate.

The Amaranthaceae and the Chenopodiaceae are more closely related palynologically to certain separate factions in the Caryophyllaceae than they are to each other. The caryophyllaceous genus *Siphonochia* and the amaranthaceous genera *Alternanthera*, *Gomphrena*, *Iresine*, *Pfaffia*, and *Tidestromia* have a very similar and very specialized pollen morphology which is not known to occur in the Chenopodiaceae. The chenopodiaceous genera *Anabasis*, *Halocharis*, *Nitrophila*, and *Traganum* have a pollen morphology that is more closely related to the caryophyllaceous genera *Cerastium*, *Drypis*, *Gymnocarpos*, *Paronychia*, and *Scleranthus* than to any members of the Amaranthaceae.

The pollen morphology of *Achatocarpus* and *Phaulothamnus* is distinct from all other Centrospermae, but the presence of betalains and the protein type sieve-tube plastid are irrefutable evidence that they do belong to this order. Their affinities within the Centrospermae and the level of recognition remain unanswered.

In each of three small families the pollen morphology is sufficiently distinct to be the key characteristic in establishing their relationships and position in the dicot hierarchy: the unstratified exine in Batidaceae; the unique (?) exine structure in Gyrostemonaceae; the zonoporate apertures and false reticulum tectum in Theligonaceae. We do not believe that the Batidaceae and Gyrostemonaceae are closely related, palynologically or otherwise; nor do we believe that the genus *Theligonum* is closely related to the Rubiaceae.

The pollen morphology of the Plumbaginaceae, Polygonaceae, and Primulaceae does not support a close relationship of any of these families to the Centrospermae nor to each other. Nevertheless, some of the results from the investigations of the first two families deserve mention: the Plumbaginaceae have only two pollen types, *Armeria* and *Plumbago*, which are remarkably distinct from each other in the structure of the exine and in the exomorphology; the Polygonaceae have great diversity in pollen types due to variation in all characteristics, apertures, surface sculpture, and the structure of the exine.

The preliminary investigation of the order Ranunculales indicates that the families Ranunculaceae, Berberidaceae, Lardizabalaceae, Coriariaceae, and Corynocarpaceae are not closely related on the basis of pollen morphology.

The Ranunculaceae have very uniform pollen with a spinulose and punctate/perforate tectum which closely resembles that found in the Centrospermae. The only taxa which do not have this tectum are *Helleborus*, *Hydrastis*, *Paeonia*, and *Trollius*.

The pollen morphology of the Berberidaceae s.l. is much more diverse and supports in part the concept of the family as closely related groups of genera. The very primitive pollen found in *Berberis* and *Mahonia* reinforces their treatment as a separate family. *Nandina* has distinctive pollen which could be used to support separate family status. Most of the remaining genera have a pollen morphology similar to various species in the Old World genus *Epimedium*, and, while all are not equally or closely related, it is a more natural grouping than previously thought. The pollen of *Diphylleia* and especially of *Podophyllum emodi* is distinct in the Berberidaceae s.l., and from all other taxa examined in the framework of these studies.

Although the pollen morphology of Coriariaceae does not have the diagnostic features found in some of the other small families, it could provide the most efficient means to evaluate the suggested relationship to the Simarubaceae. We do not believe that Coriariaceae belongs to the order Ranunculales.

For Corynocarpaceae the unusual characteristics of the pollen, especially the poorly differentiated structure of the exine, eliminate any close tie to the Ranunculales but do offer great potential as key characteristics.

For the most part the pollen of the Dilleniaceae appears to have limited value as a taxonomic parameter due to the wide and overlapping variation found in the larger genera, *Dillenia*, *Hibbertia*, *Tetracera*, etc. The close relationship attributed to *Actinidia*, *Clematoclethra*, and *Saurauia* on other bases is supported by their pollen morphology, but the distinction is not very great.

The pollen morphology of the Lardizabalaceae is relatively uniform and unspecialized and does support the present concept of the family.

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